THE QUARTERLY REVIEW *of* BIOLOGY

VOLUME IV
1929

BOSTON UNIVERSITY
COLLEGE OF LIBERAL ARTS
LIBRARY

Published by
THE WILLIAMS & WILKINS COMPANY
BALTIMORE
U. S. A.

Biology - Per.

General

Bound June 1930

THE QUARTERLY REVIEW OF BIOLOGY

RAYMOND PEARL, *Editor*
The Johns Hopkins University

ASSISTED BY

R. W. HEGNER
Contributing Editor

BLANCHE F. POOLER
Assistant Editor

JOHN RICE MINER
Assistant Editor

The Johns Hopkins University

41479

ADVISORY BOARD

ANATOMY	LEWIS H. WEED	*The Johns Hopkins University*
ANTHROPOLOGY	A. L. KROEBER	*University of California*
BEHAVIOR AND COMPARATIVE PSYCHOLOGY	K. S. LASHLEY	*Institute for Juvenile Research*
BOTANY	IRVING W. BAILEY	*Harvard University*
CYTOLOGY	EDMUND B. WILSON	*Columbia University*
ECOLOGY	WILLIAM MORTON WHEELER	*Harvard University*
EMBRYOLOGY	E. G. CONKLIN	*Princeton University*
EXPERIMENTAL MORPHOLOGY	ROSS G. HARRISON	*Yale University*
GENERAL PHYSIOLOGY	LAWRENCE J. HENDERSON	*Harvard University*
	G. H. PARKER	*Harvard University*
GENETICS	R. A. EMERSON	*Cornell University*
	T. H. MORGAN	*California Institute of Technology*
GEOGRAPHICAL DISTRIBUTION AND TAXONOMY	ALEXANDER RUTHVEN	*University of Michigan*
PALEONTOLOGY	JOHN C. MERRIAM	*Carnegie Institution*
ZOOLOGY	FRANK R. LILLIE	*University of Chicago*

QH
301
Z261
v.4

CONTENTS

No. 1, March, 1929

Biometrical Studies on Variation and Race of the Honey Bee (*Apis mellifera* L.) PAGE
W. W. Alpatov 1
Experimental Studies of Bird Malaria ..... *Robert Hegner* 59
Mendelian Inheritance in Fish ..... *H. B. Goodrich* 83
The Chemical Senses of Insects ..... *D. E. Minnich* 100
On Death from Low Temperature and Cold Resistance of Plants
Gunnar Nilsson-Leissner 113
New Biological Books:
Brief Notices 118

No. 2, June, 1929

The Neurofibril Hypothesis ..... *G. H. Parker* 155
A Century of Study upon the Development of the Eutherian Vena Cava Inferior
Franklin P. Reagan 179
Respiration in the Insects ..... *M. O. Lee* 213
The Palaeomorphology of the Human Head. Ten Structural Stages from Fish to Man. Part II. The Skull in Norma Basalis ..... *Wm. K. Gregory* 233
Populations of Ant Mounds ..... *E. A. Andrews* 248
New Biological Books:
Brief Notices 258
Editorial Note 297

No. 3, September, 1929

The Cytology of Glandular Secretion ..... *Robert H. Bowen* 299
The Influence of the Thyroid Gland and Hypophysis upon Growth and Development of Amphibian Larvae ..... *Bennet M. Allen* 325
Thyroid and Growth ..... *Frederick S. Hammett* 353
How Large Is the Mammalian Egg? ..... *Carl G. Hartman* 373
Systematic Biology and the Mutation Theory ..... *G. F. Ferris* 389
Effect of Climatic Factors on Suction Force ..... *Tsi-tung Li* 401
New Biological Books:
The Mechanics of Teleology ..... *Joseph Berkson* 415
Brief Notices 420

No. 4, December, 1929

The Nutritial Activities of the California Woodpecker (*Balanosphyra formiscivora*) ..... *William E. Ritter* 455
The Cytology of Glandular Secretion (concluded) ..... *Robert H. Bowen* 484
Studies on the Physiology of a Gene ..... *R. A. Brink* 520
The Determination of the Neural Plate in Urodeles ..... *F. G. Gilchrist* 544
New Biological Books:
Brief Notices 562
The Cost of Biological Books in 1929 ..... *John R. Miner* 598
Index to Volume IV 601

VOL. IV, No. 1 MARCH, 1929

THE QUARTERLY REVIEW *of* BIOLOGY

BIOMETRICAL STUDIES ON VARIATION AND RACES OF THE HONEY BEE (APIS MELLIFERA L.)

BY W. W. ALPATOV

The Institute for Biological Research, Johns Hopkins University

INTRODUCTION

THE purpose of the present paper is to bring together in a systematized form numerous data on the variation of the honey bee accumulated during the last five years, mostly by Russian investigators. Although the insects have been for years among the favorite objects for the discussion of variation little has been done with them along exact biometrical lines.

The honey bee may be considered an insect whose biometry is at the present moment better known than that of any of the others, and may be compared with *Drosophila*, the best known animal from the genetical point of view. G. A. Koshevnikov (33) was the first zoologist who introduced exact measurement of different parts of the exoskeleton of the honey bee as a method of study. From a statistical point of view this attempt was very incomplete because of the restricted number of observations made by this investigator. To a similar category must be referred many attempts to study the variation of the honey bee tongue, published during 1900 and 1901 in the leading American beekeeping magazines like *Gleanings in Bee Culture*. Other early articles such as those of Kulagin (35) and Martynov (38) belong to the same group of inexact papers on variation problems in the honey bee.

At this pioneer period of work in the variation of the honey bee the development of biometry in general was not high enough, and the appreciation of the biologists was also not keen enough for it to prove a useful tool in the field of variation of the honey bee. The article of Chochlov (22), a student of Professor Koshevnikov, can be considered as a new step toward the solution of our problem. This author started to measure considerable numbers of bees and to calculate biometrical constants. His measurements of the bee tongue include 1899 individuals belonging to six races, each race being represented by three colonies. The interpretation of the biometrical constants,

BOSTON UNIVERSITY
COLLEGE OF LIBERAL ARTS
LIBRARY

given without sufficient experience, challenged Philiptschenko (66) to devote a special paper to the recalculation and discussion of Chochlov's data. The conclusions of both of these authors are that different bee races have specific average tongue lengths. A. S. Michailov (39) compared Chochlov's data with his own measurements of three hundred bees from Tcherepowetz, North Russia, and the measurements obtained by him from the Tula Apicultural Station. He pointed out that the tongue length of bees in the plain of European Russia changes from the north to the south, showing a regular increase in the south. Michailov's publication stimulated the author of the present paper to work out statistically all the measurements available at that time (3).

In the year 1924 the author of the present article began on a very large scale to collect bees from all parts of Russia and Caucasus. Several Russian apicultural experimental stations like Tula, Kasan, and Kharkov, as well as private investigators, turned over their numerous measurements for biometrical computations. The work of the author of this article was closely connected with the Zoological Museum of the University of Moscow (Director, Prof. G. A. Koshevnikov) and was financed by the Bureau of Experimental Stations of the Russian Department of Agriculture. At the conference of the Russian Apicultural Experimental Stations held in Moscow in 1925, a special agreement was established concerning the distribution of problems among the apicultural research institutions in Russia. The Zoological Museum took over the problems of geographical variation, and the Tula Experimental Station, with which A. S. Michailov has been affiliated since 1925, worked out a very elaborate plan of investigation of the influence of different factors on the variation of the honey bees of a given apiary. Numerous papers of Michailov and of the author published since 1924 will be discussed in systematized form later on. Thanks to the obtaining of a research fellowship from the International Education Board, the author had the opportunity to come over to the United States of America. The whole summer of 1927 was spent in the hospitable laboratory of Professor Phillips at Cornell University. His kind help in procuring the necessary material made it possible to work out the variation of the races of the honey bee cultivated in the United States. The final calculations and preparation of the manuscript were done under Dr. Raymond Pearl, to whom we are deeply indebted for many valuable suggestions and criticisms.

COLONY VARIATION AS A BASIS FOR RACIAL STUDIES IN SOCIAL INSECTS

One of the most important facts which must be born in mind in every biometrical investigation on animals living in colonies is the family variation, that is, the differences between the characteristics of the colonies. It has been shown by several investigators, Thomson, Bell and Pearson (76, 77), Warren (79), Arnoldi (17), and Palenitschko (62) that in different groups of social insects the variation of single families is smaller than the variation of the whole population. Table 1 shows that the arithmetical means of single families differ considerably. The same can be seen in Figure 1, where variation curves of six of these Kharkov colonies are represented. If we sum up the coefficients of variation of all the colonies and divide the sum by the number of colonies we shall get a constant showing the average variation of the colony. In the case of the Kharkov apiary it will be equal to 1.56, while the coefficient of variation for the frequency distribution

representing all 800 bees is equal to 1.95, as can be seen from Table 1. Hence, expressing 1.56 in per cent of 1.95 we get 80 per cent. That is, we can say that the mean variability of the colony is equal to 80 per cent of the total variability of the apiary. We have calculated the expression of colony variation in per cent of the variation of the apiary for different apiaries. The results are represented in Table 2.

The same conclusion as to the hereditary origins of family differences can be drawn from the observation of Miss T. Dementiewa (24), who has bred the offspring of single females of the fresh water crustacean *Cyclops strenuus* Fisch. under uniform conditions as far as possible. Judging by analogy it may be supposed that in the colony differences of bees, heredity plays an important rôle. On the other hand one must bear in mind that in the bee as

TABLE 1

Means and coefficients of variation of the tongue length of eight colonies of the apiary of the Kharkov Apicultural Experimental Station. One hundred bees have been measured from each colony

(From Alpatov, 1927)

Mean in mm.....	6.423±.007	6.501±.009	6.506±.006	6.541±.007	6.544±.008	6.558±.005	6.608±.007	6.667±.007	6.549±.003
Coefficient of variation	1.68 ±.08	2.06 ±.10	1.30 ±.06	1.52 ±.07	1.72 ±.08	1.22 ±.06	1.47 ±.07	1.53 ±.07	1.95 ±.03
Number of the colony	20	1	3	11	9	7	1	8	All bees together

TABLE 2

Average colony coefficients of variation expressed in per cent of the coefficients of variation of the whole apiary

LOCALITY	AVERAGE VARIABILITY OF A COLONY	VARIABILITY OF THE WHOLE APIARY	PER CENT
Kasan Apicultural Experimental Station	1.78	2.53±.04	70.3
Moscow Apicultural Experimental Station	2.01	2.13±.03	94.8
Tula Apicultural Experimental Station	1.50	2.04±.02	73.5
Kharkow Apicultural Experimental Station	1.56	1.95±.03	80.0
Nizhni Nowgorod Zootechnical Station	1.91	2.37±.03	80.6
Jaroslawl District (private apiaries)	1.59	1.87±.03	85.0
Perm University Farm Apiary	1.75	1.83±.02	95.6

The ratios for the Moscow and Perm bees stand apart, showing the great homogeneity of the bees of these apiaries. In regard to the peculiarity just described the honey bee has analogies in other groups of animals which have been studied from the point of view of variability of families. The most exact investigations on family variation are those of J. Schmidt, who did extensive work on a North Atlantic viviparous fish *Zoarces viviparus* L. (71). It has been shown by this author that the differences between families are hereditary.

well as in other animals the conditions of development (temperature, food, size of cells and so forth) have a certain influence on the organism. In a recently published article Michailov (55) has shown that brood of the same origin developed in two colonies differing in their average tongue length develops into adult bees approximating in tongue length to their nurse colonies. His data in recalculated form are shown in Table 3.

It is interesting to note that in the honey bee the relation of the average

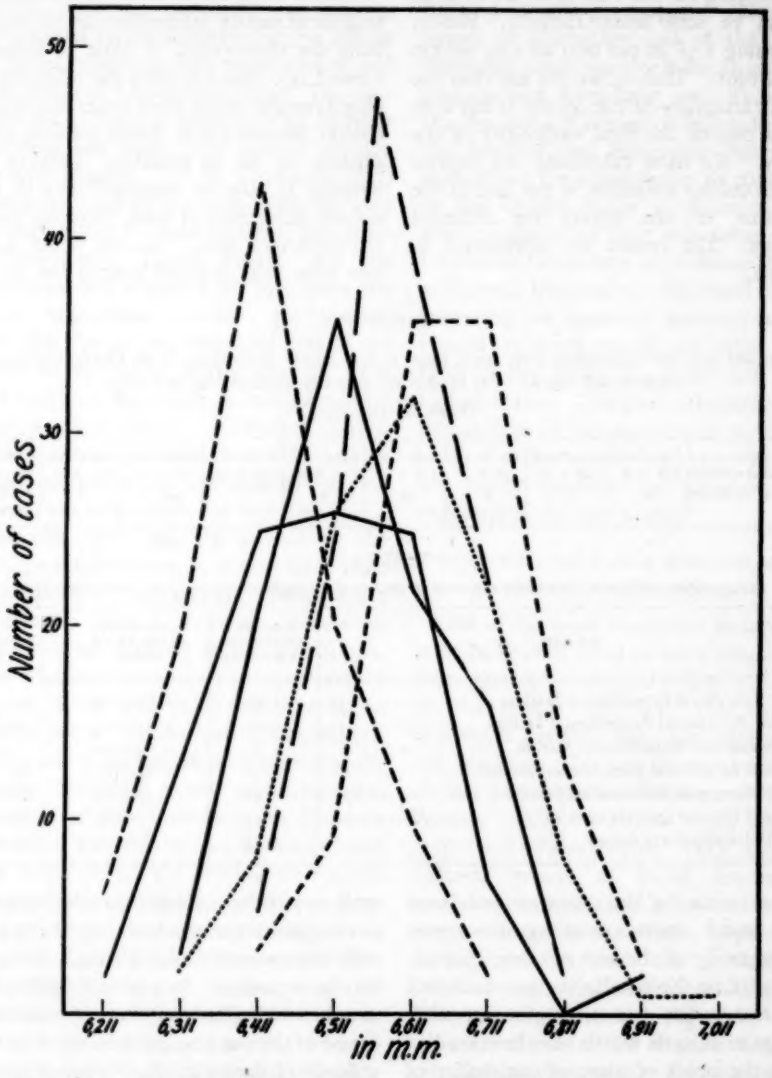


FIG. 1. VARIATION CURVES OF THE TONGUE LENGTH OF SIX COLONIES FROM THE KHARKOV EXPERIMENTAL APICULTURAL STATION

Vertical axis represents the actual number of individuals. (Based on data published by Alpatov, 1927.)

colony variation to the apiary variation is expressed by comparatively very high values of the ratio (70–95 per cent). For other animals the values are much lower: for *Aphis*, 60 per cent (Warren, 78); for *Zoarces*, 56 per cent (Schmidt); for

Vespa vulgaris, 49.6 per cent (Pearson and others); for *Termes*, 43 per cent (Warren); and 72–91 per cent for different measurements in *Cyclops* (Dementiewa). It seems to us that the most probable explanation of the difference in the value of the percentage expression of individual and racial variation between the honey bee and almost all wild animals (except *Cyclops*) is that in the honey bee we compare the hereditary relationship of the queens of the apiary. If the apiary contains many swarms obtained by inbreeding within narrow limits the colonies will be very much alike, and the colony variability will be reduced. At the present moment, with no adequate knowledge of the heredity of quantitative characters in bees, we can only make hypotheses about the comparative importance of internal

TABLE 3

Physical characteristics of bees developed in the maternal colony and of bees developed from eggs transferred to another colony. One hundred bees in each sample

(Recalculated from Michailov, 1918)

ORIGIN OF THE EGGS	EGGS OF THE QUEEN OF THE COLONY N 111				EGGS OF THE QUEEN OF THE COLONY N 5			
Place of development	Developed in the colony N 111		Put for development into colony N 5		Developed in the colony N 5		Put for development into colony N 111	
	Mean	Coefficient of variation	Mean	Coefficient of variation	Mean	Coefficient of variation	Mean	Coefficient of variation
Tongue.....	6.233±.007	1.67±.08	6.112±.007	1.65±.08	6.088±.006	1.50±.07	6.141±.005	1.32±.06
Length of the wing.	9.250±.010	1.57±.07	9.107±.008	1.35±.06	9.080±.008	1.36±.06	9.201±.008	1.35±.06
Width of the wing.	3.107±.004	1.76±.08	3.039±.004	1.84±.09	3.088±.004	1.98±.09	3.129±.004	1.99±.09
Third and fourth tergum...	4.704±.006	2.03±.10	4.617±.006	1.84±.09	4.658±.006	1.94±.09	4.690±.006	1.88±.09
Number of hooks....	21.41±.11	7.85±.37	21.51±.11	7.88±.38	20.59±.13	9.14±.44	20.65±.13	9.40±.45
	PROPORTIONS*							
Tongue....	132.55±.22	2.45±.12	132.42±.21	2.30±.11	130.74±.20	2.28±.10	130.98±.19	2.13±.10
Wing length	196.72±.30	2.30±.11	197.31±.27	2.05±.10	194.99±.26	2.00±.10	196.24±.28	2.09±.10
Wing width	33.59±.03	1.51±.07	33.37±.03	1.51±.07	34.01±.04	1.60±.08	34.01±.04	1.61±.08

* The explanation of the method of calculating the proportions will be given further on (p. 11).

variation of a family with the variation of a comparatively limited group of individuals representing the population—bees belonging to one apiary and very likely connected with each other by different degrees of blood relationship. In the case of wild animals we compare the variation of the family with the variation of the whole race. The hereditary homogeneity of an apiary depends a great deal upon the and external conditions which produce the observed differences among colonies.

In our paper (with F. A. Tjunin, 4) the attempt was made to show that the colonies differ from each other not only in the averages of their characteristics but also in the coefficients of correlation between the characteristics. Table 4 represents an example, in which the means of the mentum and ligula of two

colonies of bees of the Tula Apicultural Experimental Station give no statistical significant differences, while the correlations of the given characters in the two colonies are quite different.

The general conclusion reached from the family variation investigations is that the family is the lowest taxonomical grouping, characterized not only by its averages but by the manner of correlation of one part of the body with another. In that regard we agree perfectly with the conclusion drawn by J. Schmidt (71): "The individual offspring analyses showed that the smallest unit hitherto considered 'race' can be resolved into still smaller elements expressed by the averages of the offspring samples. The minor elements may differ widely one from another, and also from the average of the population (race), but when taken together as a whole, they present the picture of the race, as this is expressed by our population analyses."

The just discussed colony variation among bees has a very high importance in relation to the methods of racial investigation in this form. As early as 1924 we (2) discussed the same problem in relation to the taxonomy of the ants. The conclusion was that, owing to the fact that the colony variation represents only a part of the racial variation, we must collect for investigation individuals taken not from one nest but from as many colonies as possible. The following procedure illustrates the conclusion just drawn.

We had in our possession 2500 cards with tongue lengths of bees from ten colonies of Tula bees. The cards were kept in separate envelopes, representing hives of the given apiary. From each envelope a sample of five cards was taken at random. This was repeated twice and the constants of the two distributions as well as of a combined distribution including one hundred bees were

TABLE 4

Biometrical constants of two colonies of bees of the Tula experimental station

(From Alpatov and Tjunin, 1925)

	MEANS OF THE MENTUM IN MM.	COEFFICIENT OF CORRELATION BETWEEN MENTUM AND LIGULA	MEAN OF THE LIGULA IN MM.
Colony No. 53	1.604±.0013	0.349±.034	3.952±.0029
Colony No. 83	1.609±.0021	0.638±.029	3.957±.0033
Differences between the constants and $R = \frac{\text{Diff.}}{\text{P.E.}}$	0.005±.0025	0.289±.046	0.005±.0044
	R = 2.0	R = 6.3	R = 1.1

TABLE 5

Biometrical constants of samples of Tula bees

(From Alpatov, 1927)

	MEAN	STANDARD DEVIATION	COEFFICIENT OF VARIATION
First sample 5 bees from each colony	6.141±.014	0.152±.010	2.28±.15
Second sample 5 bees from each colony	6.231±.013	0.132±.009	2.12±.14
Two samples added together	6.236±.009	0.136±.007	2.20±.10

calculated. Table 5 represents the constants obtained.

Comparing the data based on these samples with the average length of Tula bee tongues calculated from the whole available material, consisting of 2500 bees, we see that the latter mean, being equal to 6.220 ± .002, differs from those in Table 5 only in the second decimal place.

tion from the true mean length of tongue of the Tula bees than did the sample of 5. The values differ in the first decimal place. This fact sets before us a very important requirement concerning the collecting of material for racial investigations on bees. The ideal condition would be to take all the individuals from different colonies, or at least to make the number

TABLE 6

Biometrical constants of samples of Tula bees, three colonies in a sample

(From Alpatov, 1927)

NUMBER OF THE COLONIES	NUMBER OF INDIVIDUALS	MEAN	STANDARD DEVIATION	COEFFICIENT OF VARIATION
10, 44, 83	600	6.191±.004	0.136±.003	2.20±.04
83, 1, 26	700	6.202±.003	0.130±.002	2.10±.04
6, 26, 52	800	6.289±.002	0.098±.002	1.59±.03
10, 44, 49	700	6.213±.003	0.100±.002	1.65±.03
6, 42, 52	800	6.335±.002	0.103±.002	1.54±.03
53, 52, 83	700	6.122±.003	0.129±.002	2.10±.04

Averages were next calculated taking bees belonging to groups of colonies taken at random. It was decided to take three colonies in the group, this number being used in racial investigations by Chochlov (22) and Michailov. The accompanying Table 6 shows that the constants obtained, in spite of the very large number of individuals (600–800) give a higher deviation of colonies not less than ten. Conclusions based on a smaller number of colonies belonging to a given race may give a completely false conclusion as to the true picture of the racial characteristics. We have tried in all our work to follow the principle just prescribed, unless the lack of material compelled us to restrict the number of colonies.

TECHNIQUE AND MATERIAL

Turning our attention to the biometrical technique we shall give here only the final stage of its development. The most important sources describing the methods of measuring the tongue length are papers of Chochlov (22) and Loginov (37). The best method to ensure that the tongue shall be fully extended is to kill the bees (slightly anesthetized by means of the usual anesthetics adopted in entomological practice—ether, calcium cyanide and others) by dropping them into boiling water. This method was used in all investigations on the tongue length of Russian bees. Killed bees may be preserved in 70 per cent alcohol, or may be immediately macerated in a 5 per cent solution of KOH until the muscles are dissolved. Dissected tongues are measured usually in water or in 70 per cent alcohol. If they have to be preserved for a while a very convenient medium is glycerin jelly or simply glycerin. Practically the same results may be obtained by using the following method of preserving the material. Bees killed in a cyanide bottle are immediately placed on a layer of cotton and the tongues everted by means of thin forceps. This method was used in preserving material from Abchasia (Caucasus). All measurements in the United States have been made on bees sent alive in queen cages, killed in boiling water and dissected and mounted in glycerin. It was found that the tongues measured on material which was preserved in dry condition without any precautions give a length which is about 6.5 per cent smaller than the normal. Our material on Russian and Caucasian bees (other than those from Abchasia) was sent to us dry in packages and was not used therefore for extensive measurements of the tongue length. The material on Italian bees from Italy was killed in boiling water and preserved in 70 per cent alcohol up to the moment of maceration in 5 per cent solution of KOH (10–15 minutes of boiling) and dissection.

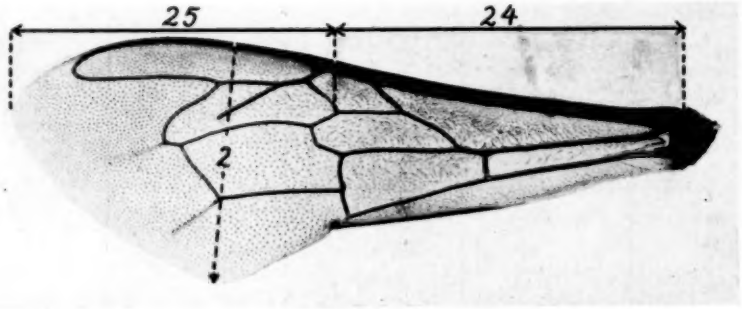


FIG. 2. MEASUREMENTS ON THE WING
The wing shows the intercubitus vein incompletely developed. (From Alpatov, 1928.)

In our study on Middle Russian and Ukranian bees twenty-five different characteristics were measured. In the subsequent work on other bee races, for the sake of saving time, eight of these measurements were omitted. Therefore in our present discussion we shall consider only those in the following list. In this list the numbering of the characters remains unchanged from that in our paper (9) mentioned above. This makes it easier

to compare the old measurements with new ones.

(2) The width of the right wing (see Fig. 2).
(24) Proximal length of the wing (See Fig. 2).
(25) Distal length of the wing (See Fig. 2).
(3) Number of hooks on the hind wing.
(16) Length of the submentum measured along the median line (See Fig. 3).
(15) Length of the mentum (See Fig. 3).
(14) Distance from the distal end of the mentum to the narrowing on the ligula (See Fig. 3).
(13) From the narrowing to the end of ligula (See Fig. 3). (This double measuring of the ligula was used by the author during his work in Moscow, where a convenient magnification permitting the measurement of the whole length of the ligula at once was not available. During our work in the United States such a magnification was found and used.)
(8) Second sternum (See Fig. 4).
(22) Maximal length of the first wax sternum (See Fig. 5).
(21) "Length" of the first wax gland surface (See Fig. 5).
(10) Width of the first wax gland (See Fig. 5).
(11) Third tergum of the abdomen. (The first tergum of the abdomen represents a convex scale; the second, being under the cover slide, is apt to give as a rule numerous clefts; the third is therefore the most convenient one. This was also proposed by Armbruster (16). (See Fig. 7.))
(5) Length of the basal joints of the tarsus (See Fig. 6).
(4) Length of the tibia. (In case the upper end of the tibia cannot be seen distinctly enough, a slight pressing on the cover slide makes the joint easily determinable.)
(23) Length of the femur (See Fig. 6).
(26) Length of the yellow stripe along the front edge of the third tergum.

In our work on Middle Russian and Ukranian bees (9) we measured the yellow band on the second abdominal tergum, expressing the length of the band as per cent of the length of the whole tergum. In our investigation of other races, and particularly light colored ones, it was decided to measure the yellow band on the third tergum, the second one being sometimes completely deprived of the black stripe along the hind edge. It was decided to measure the length of the

FIG. 3. MEASUREMENTS ON THE TONGUE

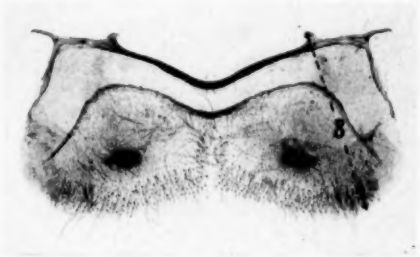


FIG. 4. MEASUREMENTS OF THE SECOND STERNUM

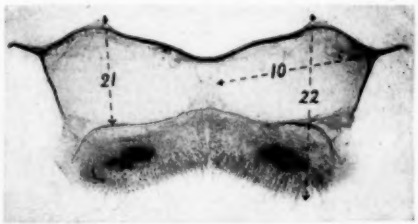


FIG. 5. MEASUREMENTS ON THE FIRST WAX STERNUM

FIG. 6. MEASUREMENTS OF THE DIFFERENT JOINTS OF THE HIND LEGS

yellow band not on the median line of the tergum but a little to the right or

to the left of it. This was done because the black band is not so sharply defined in the middle as it is a little to the sides (See Fig. 7).

The wings were cut off before putting the insects into KOH. Even a short boiling (15–20 minutes) in KOH makes the wings useless for measurement. An ocular micrometer in an N.2 ocular was used during the whole investigation. Different objectives have been used, de-

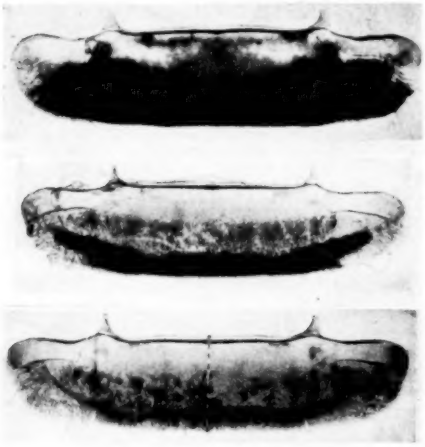


FIG. 7. MEASUREMENT OF THE THIRD TERGUM OF ABDOMEN

Third tergum of a Ukrainian bee (queen sent from Kursk) developed in Moscow, of an Italian worker bee born from an Italian queen shipped to Caucasus and of an Americanized Italian bee.

pending upon the size of the character to be measured and the length of the microscope tube. The most convenient systems were N.1 C and N.1 Reichert and N.2 Leitz. In measuring the wings in the drones a binocular was used. It must be noted that for comparative biometrical studies only very good object micrometers can be recommended. Two kinds of them must be distinguished. The first is prepared by a photographic method and is not very accurate, the other has a scale scratched by means of a dividing machine provided with a diamond.

All frequency distributions have been made in divisions of the ocular micrometer, and only afterwards have the biometrical constants been converted into millimeters. It was found very convenient to calculate the ratio-indices using the formulas given by Pearson (64) and Pearl (63).

We calculated the biometrical constants for each of our 45 groups of bees included in Table 7 separately. Afterwards, in order to get more reliable constants with smaller probable errors it was decided to group the material according to the place of origin. The biometrical constants of these groups have been deduced from the constants of the 45 groups by using the following formulas:

$$M = \frac{M_1 n_1 + M_2 n_2 + M_3 n_3 \cdots\cdots}{N}$$

$$\sigma_m = \sqrt{\frac{n_1(\sigma_{m_1}^2 + d_1^2) + n_2(\sigma_{m_2}^2 + d_2^2) + n_3(\sigma_{m_3}^2 + d_3^2 \cdots}{N}}$$

where M is the arithmetical mean of the combined group; σ_m is the standard deviation of the combined group; n_1, n_2, n_3 . . . . represent the number of cases in separate groups; N is the whole number of cases; σ_{m_1}, σ_{m_2}, σ_{m_3} . . . . are the standard deviations in separate groups; d_1, d_2 are the deviations of separate M_1 . . . . from the general M. These formulas are given in a little different form by Yule (p. 142, 82).

Table 7 contains a list of the material worked out. The numbers from 1 to 33 correspond to the localities marked on the map (Fig. 8).

INFLUENCE OF EXTERNAL CONDITIONS UPON THE ORGANISM OF THE HONEY BEE

In this section we intend to bring together all the data available at the present moment on the influence of different

external conditions upon the organism of the honey bee. It is due to a series of investigations of A. S. Michailov that this aspect of the variability of the honey bee is getting to be more and more clear. In his investigations he gives, as a rule, measurements of only five characters: (1) the tongue length, (2) the wing length, (3) wing width, (4) the sum of the length of the third and fourth tergum, and (5) the number of hooks on the hind wings. The measurements correspond in general to the scheme adopted in our own investigations. One difference is that we did not measure the length of the fourth tergum. Furthermore we did not add our measurements of the proximal and distal part of the wing length as is done in Michailov's articles. Only in one of his papers (52) does Michailov give the constants expressed in millimeters. In all others the constants are expressed in divisions of the ocular micrometer. We find it more convenient for purposes of comparison to give the final results in the metric system. In all the tables taken from Michailov's articles we recalculated the constants, expressing them in millimeters. Previous experience demonstrated the importance of the calculation of indices for characterizing constitutional types in bees. It seemed therefore just to calculate them for Michailov's experimental bees. As it was not possible to calculate from Michailov's data the coefficients of correlation indispensible for using the index formula (Michailov's article containing only frequency distribution) we substituted for the required coefficient of correlation the mean of those obtained in our work on Middle Russian and Ukrainian bees. These averaged coefficients of correlation are as follows: $r = .136$—correlation between the length of the tongue and the length of the third tergum; $r = .203$—the correlation of the wing length and the third tergum; and $r = .593$—the correlation of the length and width of the wings. The calculated proportions, by this method, are given in Table 3, *supra*, and other tables based upon Michailov's data.

The data on the influence of different conditions upon the organism of the honey bee available at the present moment may be classified in the following manner:

(1) The seasonal variation of the honey bee.
(2) The influence of the temperature during the development of the sealed brood.
(3) Size of the cells:
  (a) bees developed in worker cells and in drone cells.
  (b) bees developed in old and new cells.
(4) Nutrition:
  (a) length of larval feeding.
  (b) age of nurse bees.
(5) Influence of the age of the imago on the dimensions of the body.
(6) Strength of the colony.

The observations on seasonal variation of the honey bee have been done by Michailov. He calculated constants for bees emerging at five different times in the breeding season during the summer of the year 1926. The bees had their development in the same comb put in the middle of the strong colony. The queen of this colony was marked in the spring so that there is no doubt that all five successive groups of bees were genetically identical.

Newly emerged bees were collected directly from the comb. The accompanying Table 8 shows that the chitin of the worker undergoes distinct changes during the summer. Especially pronounced is the difference between bees emerging during the first part of the summer (before the swarming period) and bees which emerged after July 20. The right hand column shows that the increase in size toward the end of the summer is most pronounced in the wing length; then come the characters on the abdomen, and last is the tongue. The number of hook

TABLE 7

List of the material analyzed

NUMBER	LOCALITY	RACE	NUMBER OF COLONIES	NUMBER OF INDIVIDUALS	CHARACTERS STUDIED	IN WHAT GROUP INCLUDED FOR CALCULATION OF CONSTANTS
1	Radomisl, Kiev district	*A. mellifera mellifera* L.	6	64	Wing characters	50° S. Russia
2	Valuiki, Voronezh district	*A. mellifera mellifera* L.	11	68	All characters	50° S. Russia
3	Volchansk, Voronezh district	*A. mellifera mellifera* L.	7	43	All characters	50° S. Russia
4	Rossosch, Voronezh district	*A. mellifera mellifera* L.	10	48	Wing characters	50° S. Russia
5	Kriusha, Voronezh district	*A. mellifera mellifera* L.	6	60	Wing characters	50° S. Russia
6	Rovenki, Voronezh district	*A. mellifera mellifera* L.	9	92	Wing characters	50° S. Russia
7	Rudnja, Saratov district	*A. mellifera mellifera* L.	5	50	Wing characters	50° S. Russia
8	Krasnojar, Smolensk district	*A. mellifera mellifera* L.	6	60	Wing characters	55° M. Russia
9	Basmanovo, Smolensk district	*A. mellifera mellifera* L.	7	100	Wing characters	55° M. Russia
10	Smolensk	*A. mellifera mellifera* L.	10	100	Wing characters	55° M. Russia
11	Bashkirovka, Kaluga district	*A. mellifera mellifera* L.	6	59	Wing characters	55° M. Russia
12	Lukianov, Kaluga district	*A. mellifera mellifera* L.	6	55	Wing characters	55° M. Russia
13	Bykscheevo and Romanovo, Kaluga district	*A. mellifera mellifera* L.	6	62	Wing characters	55° M. Russia
14	Malojaroslavetz, Kaluga district I	*A. mellifera mellifera* L.	6	61	Wing characters	55° M. Russia
15	Malojaroslavetz, Kaluga district II	*A. mellifera mellifera* L.	6	61	Wing characters	55° M. Russia
16	Novoje, Tula district	*A. mellifera mellifera* L.	6	60	Wing characters	55° M. Russia
17	Kashira, Moscow district	*A. mellifera mellifera* L.	10	58	All characters	55° M. Russia
18	Kolomna, Moscow district	*A. mellifera mellifera* L.	8	48	All characters	55° M. Russia
19	Zaraisk, Ryazan district	*A. mellifera mellifera* L.	4	40	Wing characters	55° M. Russia
20	Ryazan	*A. mellifera mellifera* L.	6	50	Wing characters	55° M. Russia
21	Ufa	*A. mellifera mellifera* L.	9	100	Wing characters	55° M. Russia
22	Uisk, Uralsk district	*A. mellifera mellifera* L.	6	52	Wing characters	55° M. Russia
22a	Chistopol, Kasan	*A. mellifera mellifera* L.	10	99	Wing characters	55° M. Russia
23	Stavropol, N. Caucasus	Intermediate form	?	156	Wing characters	N. Caucasus
24	Maikop, N. Caucasus	Intermediate form	many	100	All characters	N. Caucasus
25	Tiflis	*A. mellifera caucasica* Gorb.	10	50	All characters	Central Mountains
26	Svanetia	*A. mellifera caucasica* Gorb.	several	36	All characters	Central Mountains
27	Kutais	*A. mellifera caucasica* Gorb.	collected on flowers	32	All characters	Central Mountains

28a	Golovinka, Abchasia I	Intermediate forms	9	45	Wing Characters	Abchasia
28b	Schache, Abchasia II	Intermediate forms	12	60	Wing characters	Abchasia
28c	Kichmai, Abchasia III	Intermediate forms	10	41	All characters	Abchasia
29	Adler, Abchasia	Intermediate forms	about 10	66		Abchasia
30	Migri, Transcaucasus	*A. mellifera remipes* Gersch.	3	29	All characters	
31	Delidjan, Transcaucasus	*A. mellifera caucasica* Gorb.	4	40	All characters	
32	Pennsylvania	*A. mellifera ligustica* Spin.	10	50	Wing characters	Italian bees. U. S. A.
33	Kentucky	*A. mellifera ligustica* Spin.	10	50	Wing characters	Italian bees. U. S. A.
34	Alabama, I apiary	*A. mellifera ligustica* Spin.	10	50	Wing characters; ½ of the specimens were measured for all characters	Italian bees. U. S. A.
35	Alabama, II apiary	*A. mellifera ligustica* Spin.	10	50	Wing characters; ½ of the specimens were measured for all characters	Italian bees. U. S. A.
36	Ohio, I apiary	*A. mellifera ligustica* Spin.	10	50	Wing characters; ½ of the specimens were measured for all characters	Italian bees. U. S. A.
37	Ohio, II apiary	*A. mellifera ligustica* Spin.	10	50	Wing characters; ½ of the specimens were measured for all characters	Italian bees. U. S. A.
38	New York, Cornell University apiary	*A. mellifera ligustica* Spin.	10	50	Wing characters	Italian bees. U. S. A.
39	New York	*A. mellifera ligustica* Spin.	10	50	Wing characters	Italian bees. U. S. A.
40	Italy, Bologna	*A. mellifera ligustica* Spin.	10	50	All characters	
41	Caucasus (queens imported from Italy)	*A. mellifera ligustica* Spin.	7	50	Wings and tongues	
42	Ontario	*A. mellifera mellifera* L.	10	50	Wings and tongues	Black bees. U. S. A.
43	North Carolina	*A. mellifera mellifera* L.	10	50	Wings and tongues	Black bees. U. S. A.
44	Florida	*A. mellifera mellifera* L.	10	50	Wings and tongues	Black bees. U. S. A.
45	Colorado	*A. mellifera caucasica* Gorb.	10	50	All characters	

remains constant throughout the whole period covered by the observation. Turning our attention to the changes in proportions of the body we find that it is only the tongue index which shows a definite increase in the bees in late summer. We agree entirely with Michailov in the statement that in racial investigations special attention must be paid to obtaining material belonging to the same biological moment. The best time seems to be in the fall and winter. In all our original

TABLE 8

Seasonal variation of the honey bee

(From Michailov, 1927)

		JUNE 5	JUNE 29/30	JULY 20/21	AUGUST 27/28	SEPTEMBER 6/21	DIFFERENCE I-V
		I	II	III	IV	V	
Tongue length	M	6.125±.008	6.189±.006	6.280±.006	6.238±.006	6.282±.006	.157±.010
	C*	2.04±.10	1.54 ±.07	1.49 ±.07	1.48 ±.07	1.47 ±.07	R = 15.7
	N	99	99	100	96	99	
Length of the wing	M	9.175±.012	9.258±.010	9.525±.010	9.458±.008	9.590±.009	.415±.015
	C	1.88 ±.09	1.54 ±.07	1.49 ±.07	1.23 ±.06	1.47± .07	R = 27.7
	N	100	100	100	100	100	
Width of the wing	M	3.063±.005	3.095±.004	3.186±.004	3.185±.004	3.200±.006	.137±.008
	C	2.45 ±.11	2.11 ±.10	2.00 ±.10	1.95 ±.09	2.60 ±.12	R = 17.1
	N	100	100	100	100	100	
Hooks	M	22.06±.10	22.00±.10	22.02±.11	21.90±.12	22.07±.10	.01±.14
	C	6.87±.33	6.95±.33	7.12±.34	8.43±.40	6.84±.33	R = 0.0
	N	100	100	100	100	100	
Tergum (III + IV)	M	4.752±.008	4.808±.007	4.954±.007	4.916±.006	4.937±.006	.185±.010
	C	2.58 ±.12	2.06 ±.10	2.19 ±.10	1.80 ±.09	1.76 ±.08	R = 18.5
	N	100	100	100	100	100	
Tongue length: tergum (III + IV)	M	128.97±.27	128.77±.21	126.82±.21	126.93±.19	127.28±.18	1.69±.32
	C	3.06±.15	2.40±.12	2.48±.12	2.17±.10	2.13±.10	R = 5.3
Wing length: tergum (III + IV)	M	193.19±.37	192.62±.30	192.35±.31	192.45±.25	194.30±.27	1.11±.46
	C	2.87±.14	2.31±.11	2.39±.11	1.96±.09	2.05±.10	R = 2.4
Breadth of wing: length of wing	M	33.39±.05	33.43±.04	33.45±.05	33.68±.04	33.37±.05	.02±.07
	C	2.02±.10	1.72±.08	2.11±.10	1.58±.08	2.10±.10	R = 0.3

* In all tables C signifies the coefficient of variation.

measurements the material was sent to us in the latter part of the summer or immediately after wintering.

Concerning the explanation of the seasonal variation we are not able at the present moment to express a definite opinion. As will be shown later on the factors. It has been known for years that during the honey flow the bees get "fat". On the other hand in beekeeping literature are scattered numerous observations on the production of dwarf bees. Especially pronounced is this phenomenon among Italian bees, which react to the disappear-

TABLE 9

Influence of the temperature of development of the sealed brood on the adult worker bees. Colony 63

(After Michailov, 1927)

		TEMPERATURE 35°	DIFFERENCE AND $R = \frac{\text{DIFF.}}{\text{P.E.}}$	TEMPERATURE 30°
Tongue	M	5.824±.008	.230±.013	5.594±.010
	C	2.02 ±.10	R = 17.8	2.41 ±.12
	N	99		88
Length of the wing	M	8.917±.011	.284±.014	8.633±.021
	C	1.88 ±.09	R = 11.8	3.40 ±.17
	N	100		87
Width of the wing	M	3.009±.005	.009±.008	3.000±.006
	C	2.31 ±.11	R = 1.0	2.93 ±.15
	N	100		87
Number of hooks	M	20.76±.12	.15±.16	20.91±.11
	C	—	R = 0.9	—
Tergum (III + IV)	M	4.580±.007	.214±.010	4.794±.007
	C	2.39 ±.11	R = 21.4	2.17 ±.11
	N	100		90
Tongue: tergum (III + IV)	M	127.23±.25	10.50±.35	116.73±.25
	C	2.91±.14	R = 30.0	3.01±.15
Length of wing: tergum (III + IV)	M	194.79±.36	14.65±.59	180.14±.47
	C	2.72±.13	R = 24.8	3.64±.19
Width of wing: tergum (III + IV)	M	33.75±.04	1.02±.08	34.77±.07
	C	1.92±.09	R = 12.75	2.88±.15

organism of the bee can be influenced by a whole set of environmental factors. Very likely all of these change considerably during the season. At the present moment we know next to nothing about the seasonal changes of any of these factors. We are inclined to think that the feeding is one of the most important

ance of the nectar secretion even by completely discontinuing brood feeding and throwing them out of the hive.

The influence of the temperature of the surroundings on the sealed brood and nymphae was also shown by Michailov (46). The first experiment consisted in putting sealed brood into two incubators

TABLE 10

Influence of the development in drone and worker cells

(Michailov, 1927)

		WORKER BEES FROM DRONE CELLS	DIFFERENCES	WORKER BEES FROM WORKER CELLS
Tongue	M	6.367±.016	.293±.021	6.074±.013
			R = 14.0	
	C	2.98 ±.18		3.47 ±.16
	N	65		112
Length of the wing	M	9.574±.027	.250±.033	9.324±.019
			R = 7.6	
	C	2.97 ±.18		2.14 ±.14
	N	63		50
Width of the wing	M	3.238±.010	.066±.013	3.172±.009
			R = 5.1	
	C	3.25 ±.20		2.97 ±.20
	N	63		50
Hooks	M	20.25±.18	.35±.25	20.60±.18
			R = 1.4	
	C	9.26 ±.56		9.26 ±.62
	N	63		50
Tergum (III + IV)	M	5.047±.020	.211±.022	4.836±.009
			R = 9.6	
	C	4.27 ±.26		1.87 ±.13
	N	63		50
Weight in grams	M	0.1451±.010	.148±.013	0.1303±.008
			R = 11.4	
	C	10.23 ±.47		9.95 ±.44
	N	106		114
Tongue: tergum (III + IV)	M	126.36±.52	.73±.60	125.63±.35
			R = 1.2	
	C	4.89±.29		3.71±.20
Length of wing: tergum (III + IV)	M	189.99±.75	2.86±.88	192.85±.46
			R = 3.25	
	C	4.67±.28		2.49±.17
Width of wings: length of wings	M	33.83±.08	.19±.11	34.02±.08
			R = 1.7	
	C	2.82±.17		2.42±.16

running at 30° and 35°C. It did not give bees differing in any respect. In the opinion of the author this is due to the inexact regulation of the incubators, and to the fact that the sealed brood was taken into the laboratory in a comparatively advanced stage of development (in the 35° incubator the bees emerged after seven and one half days, in the 30° incubator after ten days). In the second experiment

the brood put in different temperatures was apparently just sealed. The emergence in the temperature of 35°C. began after fourteen days, and in the temperature of 30°C. three days later. Special pains were taken to expose to different conditions of temperature brood genetically identical (taken from the same part of the frame from one hive). Dishes with water put in the incubators kept the air moist.

No statistically significant differences were obtained in the first experiment; we reproduce therefore in Table 9 only the results of the second experiment. The following conclusions were drawn by Michailov: (1) the "cold" bees have a shorter tongue and wing length than the "warm" ones; (2) the "cold" bees are larger in respect to the length of terga. We add two other conclusions based on our calculations of indices: (3) the "cold" bees have *relatively* short tongues and wings; (4) the "cold" bees have *relatively* broad wings. These ambiguous results—the decrease of some characters in size and the increase in the size of the abdomen of the bees kept at low temperature, can very likely be explained by the following assumption. The period of a sealed brood consists biologically of several different stages; larva, subpupa, and pupa. It is very likely that the development of the characters studied takes place during different stages of the whole development in a sealed cell. Therefore the same factor, the temperature (and very probably the changed humidity) may influence different characters in a quite different way. It would be very important to repeat the experiment, using different temperatures during the different stages of the whole development in sealed cells.

The fact that queens sometimes lay fertilized eggs in drone cells, which lead to a development of worker bees in unusually large cells, has been reported several times in the beekeeping literature. Years ago a Russian scientist Martynov (38) attempted to show that the worker bees developed in drone cells have a longer tongue than those developed in worker cells. Michailov (52) took occasion to study this comparatively rare abnormality in the egg laying activity of the honey bee. Table 10 represents his results. In the original form the constants were provided with mean errors. We calculated probable errors which are used throughout our whole investigation.

We see that in all measurements the bees developed in larger cells exceed the controls developed in regular worker cells. The proportions of the body remain unchanged.

Very close to the experiment just described is another experiment consisting in putting in one hive combs of different age (Michailov, 46). It is a popular opinion among beekeepers that in colonies where the combs are old and have been used for brood rearing for many generations the emerging bees are small. Two separate experiments were carried out. The one where the difference between the size of the two groups of cells was not very pronounced did not give definite differences in body measurements. On the other hand the experiment in which the colony N 112 was taken gave very clear results. After the experiment was over the combs were filled with paraffin and longitudinal and cross sections were prepared with a microtome. The measurements of the sections give the material for judging the dimensions of the cells and the number of generations which had their development in the cells before the experiment. Table 12 shows these data. It can be seen that the number of cocoons for the dark comb is 16.1. That means that at least 15 generations

have lived there before the generation which was taken for measurement. Another peculiarity of old combs is a deeper and narrower cell. Table 11 shows the differences in physical characteristics of bees developed in old and new combs. All characters show a smaller size in bees developed in the narrower cells. Even the number of hooks, which is usually very constant under the influence of different environmental factors, here shows a pronounced decrease. As for the proportions, the smaller, dark comb bees have a relatively longer tongue than the white

TABLE 11

Influence of age of the comb (white and dark combs) on worker bees

(From Michailov, 1927)

		WHITE COMB	DIFFERENCE AND $R = \frac{\text{DIFF.}}{\text{P.E.}}$	DARK COMB
Tongue	M	6.275±.012	.065±.016 R = 4.1	6.210±.010
	C	2.50 ±.13		1.63 ±.08
	N	79		100
Length of the wing	M	9.425±.016	.193±.017 R = 11.4	9.232±.010
	C	2.47 ±.12		1.67 ±.08
	N	96		99
Width of the wing	M	3.151±.005	.057±.006 R = 9.5	3.094±.004
	C	2.35 ±.11		1.88 ±.09
	N	96		99
Hooks	M	21.79±.12	.84±.16 R = 5.25	20.95±.10
	C	7.96±.39		6.96±.33
	N	97		99
Tergum (III + IV)	M	4.830±.010	.139±.012 R = 11.6	4.691±.006
	C	2.95 ±.14		2.03 ±.10
	N	97		100
Tongue: tergum (III + IV)	M	130.02±.34	2.40±.40 R = 6.0	132.42±.22
	C	3.60±.18		2.42±.12
Length of wing: tergum (III + IV)	M	195.28±.46	1.59±.55 R = 2.9	196.87±.31
	C	3.44±.17		2.35±.11
Width of wing: length of wing	M	33.44±.05	.08±.06 R = 1.3	33.52±.04
	C	2.18±.11		1.61±.08

comb ones. Both experiments with drone cells and the dark combs show the influence of larger cells in increasing the dimensions of the bee's body.

Turning our attention to nutrition, we must emphasize that in the development of the honey bee nutrition plays an extremely important rôle. Besides that, we must remember that it is a change in nutrition which produces intermediate forms between the worker bee and the queen, as was discovered by Pastor Klein (see 18 and 34), Koshevnikov (34) and Götze (27), and Becker (18). Our paper (14) is also devoted to the discussion of this problem.

TABLE 12

Differences between the white and dark combs used in the colony N. 112

(From Michailov, 1927)

	AVERAGE NUMBER OF COCOONS	AVERAGE DIAMETER OF THE CIRCLE INSCRIBED IN THE CROSS SECTION OF THE CELL (IN MM.)	AVERAGE DEPTH OF THE CELL (IN MM.)
White comb.....	1	5.129	11.365
Dark comb.....	16.12	4.827	11.841

During the author's residence at Cornell University (1927) an attempt was made to study the influence of under-nourishment of larvae upon the characteristics of adult bees. The experiment consisted in putting the unsealed brood in an incubator running at 34.5°C. The brood was taken from a comb approximately one day before normal sealing. On the following day when the cells situated in the neighborhood of the place from which a piece of comb had been taken the day before had been sealed by the bees, they were also put in the incubator, serving as control. The pieces of comb with unsealed larvae put in the incubator were covered with pieces of artificial comb foundation as a substitute for the natural capping by working bees. The larvae wove cocoons as usual and the emerging bees were collected according to the above described rules and preserved in alcohol. The bees emerging from the brood which was not sealed normally apparently did not get food enough, as compared with brood sealed by worker bees at the normal time. Table 13 shows that the absolute dimensions of characters measured on experimental underfed bees are smaller than in the controls. Even the number of hooks is reduced under the influence of underfeeding. The indices were calculated according to the scheme used in all our racial investigations (see below) and do not show any changes in proportions of the body of the experimental insects as compared with controls. This experiment has already been mentioned in our paper on the variation of the hooks (11) in connection with the occurrence in experimental bees of a very high percentage of individuals with an incomplete development of the second intercubitus vein.

Recent investigations of Rösch (70) have shown that among the workers of a bee colony there exists a very definite division of labor. In the feeding of the brood, bees 6–13 days old are engaged. A biometrical test of this conclusion has been made by Michailov in the following experiment. A rather strong colony, No. 121, was moved, in the middle of a good sunny day, from its usual place, on which was set an empty hive provided with frames with pollen and honey. The queen of the colony was transferred to the new hive and kept in a cage until the sealing of the experimental brood took place. All the bees of the colony N 121 which had been in the field or had left the old colony after the transfer, came back to the place where the colony used to stay

TABLE 13

Worker bees developed from underfed larvae compared with controls

CHARACTERS	CONTROL			DIFFERENCES AND $R = \frac{\text{DIFF.}}{\text{P.E.}}$	EXPERIMENTAL (UNDERFED)		
	Mean	Coefficient of variation	N		N	Mean	Coefficient of variation
8	2.307±.005	1.95±.14	44	.088±.014 6.3	28	2.219±.013	4.56±.41
10	2.337±.005	2.06±.15	43	.100±.016 6.25	25	2.237±.015	5.01±.48
21	1.554±.005	2.96±.21	44	.061±.011 5.5	25	1.493±.010	5.18±.49
22	2.757±.006	2.02±.15	44	.102±.016 6.4	25	2.655±.015	4.26±.41
Tongue length	6.034±.013	2.24±.16	43	.130±.024 5.4	31	5.904±.020	2.73±.23
5	2.033±.005	2.63±.19	45	.091±.011 8.2	31	1.942±.010	4.41±.38
4	3.169±.006	2.03±.14	45	.122±.015 8.1	31	3.047±.014	3.88±.33
23	2.609±.005	1.74±.12	45	.103±.011 9.4	31	2.506±.010	3.33±.29
Hooks	20.60±.15	7.33±.52	45	0.89±.17 5.24		19.71±.09	7.39±.33
25	4.353±.012	2.65±.19	45	.161±.026 6.2	31	4.192±.023	4.43±.38
24	4.696±.010	2.10±.15	45	.171±.023 7.4	31	4.525±.021	3.77±.32
2	3.115±.007	2.33±.17	45	.095±.012 7.9	31	3.010±.010	2.67±.23
26	1.852±.034	18.23 —	45	.058±.051 1.1	31	1.794±.038	17.48 —
11	2.241±.004	1.87±.13	45	.086±.010 8.6	31	2.155±.009	3.61±.31
21:22	56.36 ±.12	2.02±.15	44	.14 ±.18 0.77	25	56.22±.18	2.31±.22
5:11	90.75±.32	3.47±.25	45	.63 ±.42 1.5	31	90.12±.28	2.58±.22

TABLE 13—*Concluded*

CHARACTERS	CONTROL			DIFFERENCES AND $R = \frac{\text{DIFF.}}{\text{P.E.}}$	EXPERIMENTAL (UNDERFED)		
	Mean	Coefficient of variation	N		N	Mean	Coefficient of variation
4:11	141.45 ±.35	2.43±.17	45	.04 ±.52 0.0	31	141.41 ±.39	2.26±.19
23:11	116.46 ±.28	2.35±.17	45	.13 ±.43 0.1	31	116.33 ±.33	2.32±.20
25:24	92.70 ±.16	1.74±.12	45	.06 ±.31 0.0	31	92.64 ±.27	2.37±.20
2:24	66.39±.11	1.67±.12	45	.40 ±.23 1.7	31	66.79±.20	2.53±.22
26:11	82.65±1.52	18.33 —	45	.65±2.33 .28	31	83.30±1.76	17.42 —

before the transfer and populated the new hive. As a result of this procedure the old hive transferred to a new place was deprived of field bees, which are as a rule older than eleven days, and contained only hive bees—in other words, young bees. The opposite was the case in the new hive where only field bees were present. A piece of comb with eggs and new born larvae was taken from another colony (No. 39) and was divided into two pieces. They were then put into two hives populated by bees of different ages. The results of a biometrical investigation are shown in Table 14. The bees brought up by old nurses have larger wings and tergums than those fed by young bees. The proportions of the body show that the smaller bees fed by young nurses have comparatively long tongues. Michailov's conclusion is that the experiment does not bring any evidence in support of Rösch's conclusions. We do not believe that it is wise to attribute the differences observed to the age of the nurse bees only. The conditions in both hives were different in many respects, which is also admitted by Michailov. The absence of the queen in one of the hives (with young bees) might be responsible for many peculiarities in the behavior of the members of the colony.

We will not put much stress on Michailov's conclusions concerning the changes of bees with age (49). The experiment consisted in measuring new born bees and bees previously marked with color marks at the age of 25 days. The observed differences—reduction in the length of the tongue and in the number of hooks and increase in the wing width—might be caused not by aging but by selection, the marked bees being placed in a hive from which they could fly out and get lost.

Some very interesting statistical conclusions concerning the relationship between the strength of the colony and its average tongue length can be drawn from the material published by V. P. Michailov, Director of the Experimental Apiary of the Perm State University. He measured (57) the tongue length in 23 colonies of bees, taking about 200 individuals from each hive. The colonies were classified

as strong, middling, and weak ones. This classification has not, of course, the precision of a quantitative evaluation but nevertheless it expresses the general impressions as to the quantity of bees in the hive, the degree of working activity, etc. Calculating the coefficient of correlation between the strength and the average tongue length we obtain $r = .489 \pm .107$. We may thus conclude with tolerable certainty that the stronger colonies have longer tongues. In a recent paper (48) A. S. Michailov found that there is no correlation between the strength of the colony (number of bees in the colony) and the size of the different parts of the exoskeleton. A positive correlation was found between the strength of the colony and the average weight of bees caught at the entrance of the hive when they were ready to leave the hive, flying in the field. The coefficient of correlation was found to be $.591 \pm .080$. Michailov's calculations were based on measurements of

TABLE 14

Biometrical constants of worker bees reared by old and young nurse bees. Each group is represented by 100 specimens
(From Michailov, 1928)

		REARED BY OLD NURSE BEES	DIFFERENCE AND $R = \frac{\text{DIFF.}}{\text{P.E.}}$	REARED BY YOUNG NURSE BEES
Tongue	M	6.205±.008	.010±.011 R = 0.9	6.195±.007
	C	1.84 ±.09		1.69 ±.08
Length of the wing	M	9.307±.009	.076±.011 R = 6.9	9.231±.007
	C	1.41 ±.07		1.20 ±.06
Width of the wing	M	3.187±.004	.051±.006 R = 8.5	3.136±.004
	C	1.95 ±.09		1.81 ±.09
Hooks	M	20.36 ±.10	.52 ±.14 R = 3.7	20.88±.10
Tergum (III + IV)	M	4.814±.006	.056±.008 R = 7.0	4.758±.006
	C	1.94 ±.09		1.86 ±.09
Tongue: tergum (III + IV)	M	128.94 ±.22	1.30±.29 R = 4.5	130.24 ±.19
	C.	2.48 ±.12		2.15 ±.10
Length of wing: tergum (III + IV)	M	193.39 ±.28	.68 ±.38 R = 1.8	194.07 ±.26
	C	2.15 ±.10		2.00 ±.10
Width of wing: length of wing	M	34.24 ±.37	.27 ±.50 R = 0.5	33.97±.33
	C	1.59 ±.08		1.46 ±.07

bees from thirty colonies of the Tula Apicultural Experimental Station. This lack of agreement with our conclusions based on data collected in Perm may perhaps find its explanation in the hypothesis that the Tula colonies were more uniform in respect to their strength than those from Perm. Anyhow the question should be investigated further.

Summing up the results discussed in regard to the change of proportions of the body we can draw only one conclusion. In the cases where all characteristics of the bees affected by experimental conditions showed a decrease (influence of the age of nurse bees, small cells, season of the year), smaller bees have relatively long tongues. In the case of the influence of temperature bees with shorter wings had relatively broader wings. These conclusions may help us to explain in the future some of the racial differences in the proportion of the body of the honey bee.

GEOGRAPHICAL VARIATION OF BEES FROM THE PLAIN OF EUROPEAN RUSSIA, ITALY AND NORTH CAUCASUS

Turning our attention to the geographical variation of the honey bee we must start with races of eastern Europe because the pioneer work on geographical variation was done there. This is not owing to chance. It is easy to observe laws in the geographical changes of characters in animals when the climate and other environmental factors change regularly and gradually. Such is just the case with the plain of European Russia, while it is not so in Western Europe, which is cut up by mountain chains. It is also not without importance that the Russian plain has always been politically one country, which has a certain advantage in studying conditions from the same point of view. In that respect conditions there resemble greatly those of North America. We are inclined to think that the American scientists, having long ago been interested in the geographical variation of animals, (remember the classical work of Allen on the geographical variation of birds) would not have neglected to make investigations of the geographical variation of the honey bee, had it not been for one circumstance.

FIG. 8. MAP OF EUROPEAN RUSSIA AND CAUCASUS, SHOWING THE AVERAGE TONGUE LENGTH OF BEES FROM DIFFERENT LOCALITIES

The averages are accompanied by probable errors only in cases when the examined bees have been collected from not less than five colonies.

The whole bee population of the New World is the result of a transportation of different bee races from Europe, the honey bee not being among the animals native to America.

As was stated above the tongue was the first organ to be studied from the point of view of variability which gave evidence of the existence of geographical variation (Michailov, 39). The map in figure 8 shows the results of tongue measurements

TABLE 15

Biometric constants of the tongue length in different localities in European Russia. In the table are included only data representing measurements based on a considerable number of colonies

LATITUDE	LOCALITY	MEAN IN MM.	STANDARD DEVIATION	COEFFICIENT OF VARIATION	NUMBER OF SPECIMENS	NUMBER OF COLONIES	SOURCE
58°	Perm	6.176±.002	.1133	1.83±.02	2000	20	W. P. Michailov, 1926. Alpatov, 1927.
57½°	Jaroslawl	5.996±.003	.1421	2.37±.04	931	10	Alpatov, 1927
56¼°	Nizhni Nowgorod	6.152±.002	.1456	2.37±.03	1676	17	Kurotschkin, 1928
55¾°	Moscow	6.115±.003	.1299	2.13±.03	1000	10	Alpatov, 1927
55¼°	Kasan	6.113±.003	.1544	2.53±.04	1000	20	Loginov and Alpatov, 1926
54½°	Tula	6.220±.002	.1270	2.04±.02	2500	10	Alpatov and Tjunin, 1925
50°	Kharkov	6.549±.003	.1280	1.95±.03	800	8	Alpatov, 1927

TABLE 16

Biometrical constants for bees of Middle and South Russia, North Caucasus and Italy

CHARACTERS	CHARACTER NUMBER	1	2	3	4	$R = \frac{\text{DIFF.}}{\text{P.E.}}$ FOR THE DIFFERENCES BETWEEN THE MIDDLE RUSSIAN AND BEES FROM SOUTH RUSSIA, NORTH CAUCASUS AND ITALY		
		55° MIDDLE RUSSIA	50° SOUTH RUSSIA	NORTH CAUCASUS	ITALY	1–2	1–3	1–4
Length of the second sternum	8	2.453±.004	2.387±.005	2.391±.004	2.306±.005	10.0	10.3	24.5
Length of the first wax sternum	22	2.988±.007	2.858±.007	2.830±.005	2.732±.006	13.0	17.6	28.4
Length of the first wax gland surface	21	1.778±.005	1.631±.006	1.589±.004	1.511±.005	18.3	31.5	38.1
Width of the first wax gland	10	2.541±.006	2.423±.008	2.390±.005	2.302±.006	11.8	18.9	29.9
Length of the first tarsal joint	5	2.125±.004	2.095±.004	2.116±.005	2.081±.005	5.0	1.5	7.3
Length of the tibia	4	3.363±.006	3.293±.005	3.438±.005	3.225±.005	8.75	9.4	17.3
Length of the femur	23	2.738±.004	2.678±.004	2.777±.004	2.653±.005	10.0	6.5	14.2
Distal length of the wing	25	4.553±.002	4.499±.003	4.398±.003	4.333±.012	13.5	38.75	18.3
Proximal length of the wing	24	4.913±.002	4.871±.003	4.792±.004	4.713±.009	10.2	30.25	22.2
Width of the wing	2	3.166±.002	3.189±.003	3.071±.004	3.168±.008	7.7	23.8	0.2
Number of hooks	3	20.70 ±.04	21.08 ±.06	20.61±.06	21.51 ±.08	8.85	1.29	9.0
Length of the third tergum	11	2.345±.005	2.266±.006	2.257±.004	2.171±.005	9.9	14.7	19.2
Indices:								
21:22		59.53±.12	57.10±.13	56.15±.11	55.31±.15	13.5	19.9	22.2
5:11		90.69±.24	92.55±.26	93.79±.21	95.89±.33	5.3	9.69	12.7
4:11		143.48±.36	115.44±.41	152.40±.24	148.61±.45	3.6	20.7	8.8
23:11		116.81±.23	118.30±.32	123.00±.21	122.25±.38	3.7	20.0	12.4
25:24		92.68±.05	92.39±.08	91.67±.10	91.96±.25	3.2	9.1	2.9
2:24		64.46±.03	55.47±.05	64.50±.07	67.22±.14	16.8	0.6	23.0

on the plain of European Russia and Caucasus up to the present time. In order not to put much stress on data obtained from measurements of bees belonging to less than five colonies of a given locality the averages in this case are not provided with probable errors. It is perfectly clear that bees even of neighboring localities differ in the average length of tongue. At the same time we observe as a general rule that farther to the south the tongue is longer.

In one of our previous papers (5) (independently of Michailov, 42) we attempted to express in the form of a linear equation the relationship between the length of the tongue and the latitude of the locality. In recalculating this equation we used only

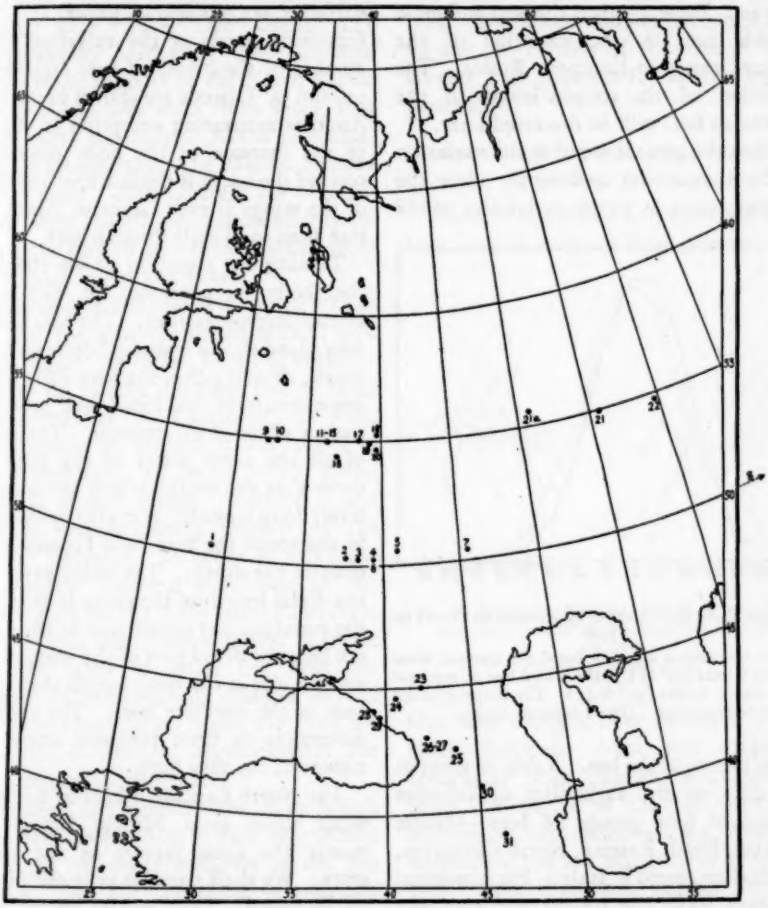


FIG. 9. MAP OF EUROPEAN RUSSIA AND CAUCASUS
The figures indicate localities where the material has been collected.

the most reliable averages of the Kharkov, Tula and Moscow bees.

This equation is as follows: $y = 10.3219 - 0.07559\,x$, x standing for the latitude of the locality and y for the length of the tongue. Table 15 gives the best and most reliable data on the variation of the tongue length in European Russia. The variation of the tongue length of the Caucasian bees will be discussed later.

When the general trend in the variation of the tongue was sufficiently clear the question arose as to the variability of the other organs of the bee. Table 16 gives us the data on the variability of different organs of four groups of bees—Middle Russian, South Russian, North Caucasian, and Italian reared in Italy. For a moment we may leave the tongue and turn our whole attention to the variation of other organs. Let us for a while omit from the discussion the North Caucasians. The first conclusion is that the southern bees are smaller than the northern ones in absolute dimensions of the body. Only the number of hooks shows a pronounced increase toward the south. The data on wing characteristics are based on very large material from different parts of European Russia. The accompanying map of figure 9 shows the localities where the material was collected. (For hook variation see our special paper, 11.) The frequency curves of the variation of the number of the hooks of bees collected at 50° and 55° latitude are shown in figure 10. Another interesting exception to the rule of the decrease of the body dimensions toward the south is the fact that the width of the wings is even larger in South Russian than in Middle Russian bees.

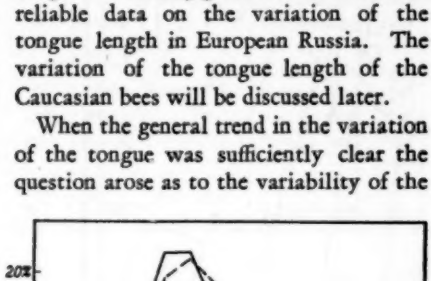


FIG. 10. FREQUENCY CURVES OF NUMBER OF HOOKS OF BEES

The continuous curve is based on material from Middle Russia (55° N.L.), the dotted line on material from South Russia (50° N.L.). The frequencies are expressed in percent. (From Alpatov, 1928).

Turning our attention to the change in the body proportions we find many interesting regularities. The index of the wax gland shows a gradual decrease in the south, showing that the bees there have a less extensively developed wax producing surface of the third sternum. The indices of all the three joints of the hind legs show that the southern bees are comparatively long legged. It is also evident that in the south the bees have broader wings than in the north. The index expressing the distal length of the wing in percent of the proximal one shows that in the southern bees the distal part of the wing plays a smaller rôle in the wing length than in the case of the northern bees. The ratios of differences to their probable errors are, however, not very high.

The North Caucasian bees as compared with those from Middle Russia give nearly the same picture as the Italian ones. We shall mention only the discrepancies found. The absolute length of the leg joint is even larger than in Middle Russians. That gives as a result an extremely high value for leg indices. We shall later on find the same characteristic picture for all Caucasian races. The North Caucasian bees do not show any increase in the relative width of the wing. We do not know at the present

moment any adequate explanation for this fact.

A preliminary report on the decrease in body size of the honey bee in southern localities was sent by us to be announced at the All German Beekeeper's Meeting on August 3–4, 1926 (see Götze, 27). Independently Michailov (40), in comparing measurements of the North Caucasian (Kuban) bees with those from Tula found that the Kuban (North Caucasus) bees are smaller than the Middle Russian (Tula) ones. Unfortunately his observations were based on measurements of bees belonging to only three colonies from the Kuban region and Tula.

Summing up the results obtained we can say that the southern constitutional type of the honey bee differs from the northern one by its smaller absolute size of body and extremities (the Caucasian bees being an exception in respect of the length of the extremities); its larger mouth parts; more developed wings (relatively); and smaller wax producing surface of the ventral segments. In order to make the statistically observed differences in the constitution of the body more instructive we prepared the schemes shown in figure 11. We want to point out that the scheme of north-south changes in the bee body constitution holds true only for localities situated in approximately the same degree of longitude.

Without any question the rules which have been observed on worker bees should be tested on other members of the bee colony. But the collection of adequate material on drones, and particularly on queens, is not a very simple matter. We attempted to compare two groups of drones from Middle and South Russia (Table 17). The southern drones are in all characters absolutely smaller than the northern ones (the differences in characters 24, 2, mentum+ligula and the number of hooks are not statistically very significant). Very interesting is the index 25:24 which is in accord with the trend observed on worker bees. The indices of the extremities show even a rather opposite trend to that found in the worker bees. We do not want to put much stress on the proportions of the drone's body, leaving this question for further investigations.

VARIATION OF THE BEE RACES CULTIVATED IN THE UNITED STATES

The bees cultivated in the United States have been introduced from Europe. The

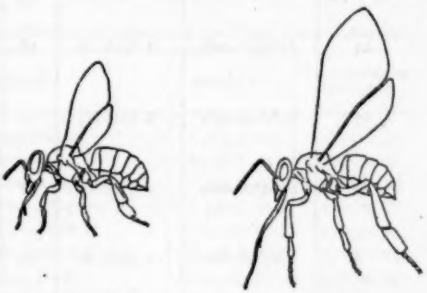


FIG. 11. SCHEMATIC REPRESENTATION OF THE NORTHERN AND SOUTHERN CONSTITUTIONAL TYPES OF BEES
(From Alpatov, 1927)

first bees brought over belonged to the black European races and originated apparently from England and Holland. Since the sixties of the last century a movement has arisen among American beekeepers toward the culture of yellow bees. Since that time, step by step, the black bees have been more and more replaced by yellow Italian bees, and partly by other light colored European races like the Cyprian. At the present time it is a difficult task to find places where the black bees are cultivated. It must further be said that the demand for yellow bees produced a strong selection of

TABLE 17

Biometrical constants of drones from Middle Russia and Ukraine

CHARACTER NUMBER	KALUGA (MIDDLE RUSSIA)		N	DIFFERENCE AND $R = \frac{\text{DIFF.}}{\text{P.E.}}$	N	N. WODOLAGA (SOUTH RUSSIA) UKRAINE	
	Mean	Coefficient of variation				Mean	Coefficient of variation
8	2.578±.006	2.47±.17	49	.112±.010 R = 11.2	46	2.466±.008	3.27±.23
22	2.918±.007	2.50±.17	49	.116±.011 R = 10.5	46	2.802±.009	3.29±.23
5	2.812±.010	2.74±.25	27	.131±.017 R = 7.7	33	2.681±.014	4.59±.38
4	4.216±.009	1.59±.14	28	.133±.017 R = 7.8	32	4.083±.014	2.86±.24
23	3.535±.008	1.67±.15	28	.137±.014 R = 9.9	31	3.398±.011	2.66±.23
25	5.801±.016	2.57±.19	41	.395±.019 R = 20.8	48	5.406±.010	2.56±.18
24	6.647±.014	1.97±.15	41	.028±.019 R = 1.5	48	6.619±.013	2.76±.19
2	4.037±.012	2.48±.21	32	.073±.019 R = 3.8	41	3.964±.015	3.56±.27
11	2.961±.011	2.86±.26	27	.048±.017 R = 2.8	33	2.913±.013	3.87±.32
mentum + ligula	3.578±.013	2.56±.27	21	.009±.031 R = 0.3	21	3.587±.028	5.28±.55
Hooks	20.22 ±.20	9.76±.69	45	.61 ±.33 R = 1.8	48	20.83 ±.26	12.00 ±.87
5:11	95.02 ±.44	3.56±.33	27	2.92 ±.69 R = 4.2	33	92.10 ±.53	4.88 ±.40
4:11	142.40 ±.45	2.47±.22	28	2.12 ±.80 R = 2.65	32	140.28 ±.66	3.95±.33
23:11	119.42 ±.42	2.79±.25	28	0.77 ±.71 R = 1.1	31	118.65 ±.59	4.13±.35
25:24	87.29 ±.26	2.78±.21	41	5.58 ±.35 R = 15.9	48	81.71 ±.23	2.89±.20
2:24	60.80 ±.22	3.03±.25	32	.71 ±.33 R = 2.1	41	60.09 ±.25	4.03±.30

strains with a very light coloration of the abdomen; this demand determined the appearance on the market of the "three banded" bees called also "golden" bees.

While working in the apicultural laboratory of Cornell University, through the help and courtesy of Prof. Phillips and various beekeepers scattered over the United States, we had the opportunity to study the bee races cultivated in this country. For tongue measurements we decided to have 50 bees from each separate apiary, taking them from ten colonies. unreasonable to expect such a rule if we remember how many queens are sent every year from the southern to the northern states. According to some estimations not less than 500,000 queen bees are sold every year by queen breeders to the beekeepers in the United States, and it is mostly in the South that the breeders have their apiaries for commercial queen breeding.

The black bees we succeeded in measuring from three localities in this country give a very similar length of tongue.

TABLE 18

Average tongue lengths and coefficients of variation of bees of different races cultivated in the United States of America

		LOCALITY	MEAN IN MM.	COEFFICIENT OF VARIATION
Italian bees	1	Pennsylvania	6.324±.009	1.55±.10
	2	Kentucky	6.166±.011	1.78±.12
	3	Alabama (apiary I)	6.332±.010	1.73±.12
	4	Alabama (apiary II)	6.340±.010	1.63±.11
	5	Ohio (apiary I)	6.419±.012	2.00±.14
	6	Ohio (apiary II)	6.396±.013	2.05±.14
	7	Ithaca, N. Y.	6.224±.012	2.00±.14
	8	New York	6.388±.010	1.69±.11
Black bees	1	Ontario	5.960±.013	2.27±.15
	2	North Carolina	5.869±.009	1.69±.11
	3	Florida	5.974±.007	1.29±.09
Gray Caucasian bees	1	Colorado	6.638±.009	1.53±.09

For measuring other characteristics bees were taken from four apiaries (two in Ohio and two in Alabama). Starting our discussion with the tongue length we see from Table 18 that the yellow bees have considerably longer tongues than the black ones. Remembering the rôle of geographical variation of the bee tongue in Eastern Europe we attempted to put the obtained averages on the geographical map (see Fig. 12). It turned out that there are no indications of a smaller size of tongue in American yellow bees in the northern parts of the country. It would be indeed They also do not show any geographical regularity comparable with that exhibited by bees in Eastern Europe. We suspected at the beginning of our work on American bees that black bees in this country would show some differences in the North and in the South. It seemed easy to imagine that the black bees imported for years into the United States would have been differentiated according to natural conditions in the South and in the North. But this is probably not the case. Figure 13 represents graphically the variation of the tongue length of bees measured in the

United States of America. The four curves below show that the variability of the tongue length of the American Italian bees is not uniform in different apiaries. For instance, the apiary from Kentucky gives only 6.166 ± .011 mm. and the two apiaries from Ohio show the highest length—6.419 ± .012 and 6.396 ± .013 respectively.

calculate the average tongue length, which is equal to 6.428 ± .005. Specimens of Italian bees reared from queens imported from Northern Italy were sent to us from Caucasus. The material was preserved in a dry condition and we have been obliged to select for measurement only specimens with well stretched ligula. The average so obtained is 6.298 ± .015,

FIG. 12. MAP OF THE UNITED STATES REPRESENTING THE AVERAGE TONGUE LENGTH OF BEES BELONGING TO DIFFERENT RACES AND DIFFERENT APIARIES

The numbers below 6.00 mm. refer to the black bees (dots in a circle), the average in Colorado to the gray Caucasian bees (triangles). All others represent the yellow Americanized Italian bee.

Comparing the tongues of the Italian bees reared in the United States with native Italian bees, which gave us the tongue length equal to 6.234 ± .010 mm., we observe that some of the American apiaries show a longer tongue than the Italians and one apiary (Kentucky) on the contrary a shorter one. We do not have at our disposal material enough to reach a sound conclusion concerning the tongue length of true Italian bees. Chochlov's measurements based on Italian bees from three colonies (N = 300) permit us to the bees belonging to seven colonies. Summing up our whole experience we conclude that the average tongue length of different strains of Italian bees varies from 6.15 to 6.45 millimeters.

In regard to other characteristics of Americanized bee races we have to turn our attention to the tables containing summarized data on all bee races (Tables 16–21).

Table 19 shows that the American Italian bees compared with Russian bees (55° and 50° of latitude) have shorter

wings, but practically the same width of wing. The index 25:24 is the same in American Italian and in Russian bees. On the other hand, the width is larger in American Italian than in Russian bees.

in that respect intermediate between the Italian born from Italian queens and black Russian and Ukrainian bees.

If we compare the American Italian with American black bees we find between them

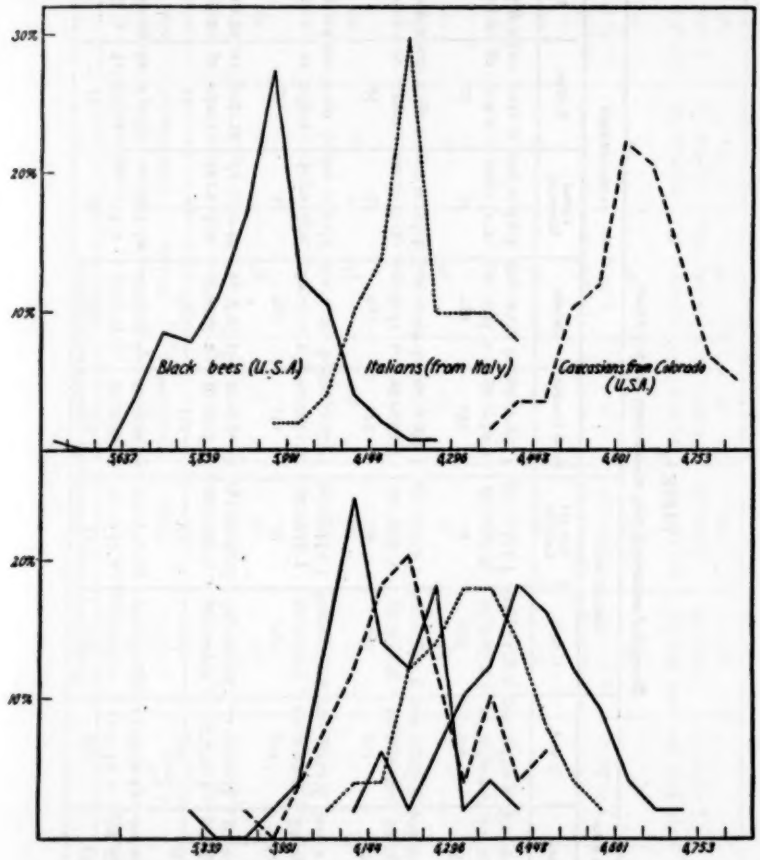


FIG. 13. VARIATION CURVES OF TONGUE LENGTH OF DIFFERENT RACES
Four lower curves show the variation of the tongue of bees from Kentucky, Ithaca, Alabama and Ohio. The frequencies are given in percent.

American Italian bees compared with Italian bees from Italian queens have larger wings in absolute dimensions (the *R* for the differences in the width is only 3.8) and relatively narrower wings, being a difference of almost the same value as between the black and Italian bees in Europe. The American black bees have longer wings (the probable error ratio is only 3.3 for the proximal length) and

TABLE 19

Biometrical constants of wing measurements and proportions

		BLACK BEES			ITALIAN BEES		CAUCASIAN BEES					
		M. Russia	S. Russia	U. S. A.	U. S. A.	Italy and Caucasus	North Caucasus	Abchasia	Central Mountains	Delidjan	Migri	Colorado U. S. A.
24	M	4.913±.002	4.871±.003	4.843±.008	4.813±.004	4.735±.006	4.792±.004	4.833±.006	4.846±.007	4.852±.013	4.685±.016	4.872±.010
	C	2.10±.03	2.18±.05	2.89±.12	2.37±.06	1.78±.09	2.03±.06	2.38±.08	2.13±.10	2.40±.18	2.35±.24	2.27±.14
	N	893	451	128	360	87	241	182	95	37	22	56
25	M	4.553±.002	4.499±.003	4.506±.006	4.448±.004	4.351±.008	4.398±.003	4.469±.005	4.511±.008	4.482±.009	4.440±.010	4.547±.008
	C	2.10±.03	2.34±.05	2.09±.09	2.24±.06	2.44±.12	1.80±.06	2.15±.08	2.32±.12	1.80±.14	1.54±.16	1.85±.12
	N	887	449	128	360	87	241	182	95	39	22	56
2	M	3.166±.002	3.189±.003	3.131±.004	3.177±.003	3.154±.005	3.071±.004	3.146±.004	3.166±.006	3.162±.009	3.158±.010	3.236±.005
	C	2.19±.04	2.43±.05	2,16±.09	2.29±.06	2.37±.12	2.14±.09	2.53±.09	2.71±.13	2.63±.21	2.11±.21	1.84±.12
	N	875	449	128	360	87	137	182	95	37	22	56
Index 25:24	M	92.68±.05	92.39±.08	93.08±.17	92.44±.09	91.91±.16	91.67±.10	92.50±.13	93.04±.17	92.40±.21	94.81±.28	93.37±.21
	C	2.32±.04	2.77±.06	3.02±.13	2.60±.07	2.41±.12	1.92±.08	2.72±.10	2.51±.13	2.04±.16	1.98±.20	2.47±.16
	N	887	449	128	360	87	141	182	86	37	22	56
Index 2:24	M	64.46±.03	65.47±.05	64.67±.10	66.03±.06	66.62±.12	64.50±.07	65.11±.07	65.34±.11	65.18±.14	67.43±.23	66.45±.13
	C	2.26±.04	2.52±.06	2.54±.11	2.39±.06	2.39±.12	1.93±.08	2.23±.08	2.53±.12	1.94±.15	2.39±.24	2.25±.14
	N	875	449	128	360	87	137	182	95	37	22	56

TABLE 20

Biometrical constants of hind leg measurements and proportions

		BLACK BEES		ITALIANS		CAUCASIANS				
		55° M. Russia	50° S. Russia	U. S. A.	Italy	North Caucasus	Abchasia	Central Mountains	Migri	Colorado U. S. A.
5	M	2.125±.004	2.095±.004	2.102±.004	2.081±.005	2.116±.005	2.087±.003	2.095±.004	2.058±.006	2.112±.004
	C	2.54±.14	2.45±.13	2.59±.12	2.70±.18	3.19±.15	2.42±.12	2.93±.14	2.40±.22	2.13±.13
	N			99	49	97	98	94	27	60
4	M	3.363±.006	3.293±.005	3.276±.005	3.225±.005	3.438±.005	3.421±.004	3.405±.005	3.314±.008	3.439±.005
	C	2.26±.13	2.02±.11	2.03±.10	1.74±.12	1.94±.09	1.75±.08	2.24±.11	1.89±.17	1.68±.10
	N			99	49	97	98	94	27	60
23	M	2.738±.004	2.678±.004	2.682±.005	2.653±.005	2.777±.004	2.741±.003	2.750±.004	2.669±.006	2.724±.003
	C	1.72±.09	2.09±.11	2.50±.12	1.78±.12	1.93±.09	1.76±.08	2.23±.11	1.69±.16	1.42±.09
	N			99	49	97	98	93	27	60
5:11	M	90.69±.24	92.55±.26	93.20±.23	95.89±.33	93.79±.21	91.77±.15	91.40±.22	92.74±.23	93.50±.23
	C	3.38±.19	3.64±.30	3.66±.18	3.53±.24	3.34±.16	2.38±.11	3.47±.17	1.88±.17	2.79±.17
	N			99	49	97	98	94	27	60
4:11	M	143.48±.36	145.44±.41	145.24±.34	148.61±.45	152.40±.24	150.46±.23	148.51±.28	149.35±.55	152.22±.27
	C	3.22±.18	3.62±.20	3.47±.17	3.16±.21	2.30±.11	2.20±.10	2.73±.13	2.85±.26	2.01±.12
	N			99	49	97	98	94	27	60
23:11	M	116.81±.23	118.30±.32	118.88±.27	122.25±.38	123.10±.21	120.54±.18	119.93±.23	120.98±.51	120.59±.26
	C	2.45±.14	3.49±.19	3.40±.16	3.21±.22	2.49±.12	2.10±.10	2.80±.14	3.29±.30	2.47±.15
	N			99	49	97	98	93	27	60

TABLE 21

Biometric constants of abdomen measurements and proportions

		BLACK BEES		ITALIANS		CAUCASIANS				
		55° M. Russia	50° S. Russia	U. S. A.	Italy	North Caucasus	Abchasia	Central Mountains	Migri	Colorado, U. S. A.
8	M	2.453±.004	2.387±.005	2.385±.004	2.306±.005	2.391±.004	2.390±.005	2.406±.004	2.341±.007	2.380±.004
	C	1.86±.13	2.30±.16	2.36±.11	2.05±.14	2.49±.12	2.21±.14	2.26±.11	2.22±.20	1.96±.12
	N			98	48	98	59	95	27	59
21	M	1.778±.005	1.632±.006	1.628±.005	1.511±.005	1.589±.004	1.633±.003	1.670±.004	1.610±.006	1.654±.005
	C	2.65±.18	3.75±.27	4.26±.21	3.47±.24	3.72±.19	2.90±.15	2.98±.15	2.86±.27	3.28±.21
	N			92	46	90	86	85	26	56
22	M	2.988±.007	2.858±.007	2.861±.005	2.732±.006	2.830±.005	2.855±.005	2.884±.005	2.789±.010	2.823±.007
	C	2.22±.14	2.45±.17	2.71±.13	2.13±.15	2.41±.12	2.27±.12	2.56±.13	2.64±.25	2.72±.17
	N			92	46	90	86	85	26	56
21:22	M	59.53±.12	57.10±.13	56.91±.13	55.31±.15	56.15±.11	57.18±.09	57.92±.11	57.75±.14	58.59±.11
	C	1.99±.14	2.25±.16	3.16±.16	2.73±.19	2.85±.14	2.27±.12	2.64±.14	3.13±.29	2.17±.14
	N			92	46	90		85	26	56
10	M	2.541±.006	2.423±.008	2.431±.005	2.302±.006	2.390±.005	2.365±.005	2.393±.005	2.337±.007	2.405±.008
	C	2.49±.17	3.29±.23	3.14±.16	2.83±.20	2.69±.13	2.66±.14	2.79±.15	2.03±.20	2.78±.18
	N			92	46	91	87	77	23	56
26	M			1.756±.021	1.076±.021	.8116±.0174	.7188±.0159	.5054±.0132	1.297±.040	.5961±.0164
	C			17.71	20.71	31.29	32.42	35.36	23.68	31.54
	N			99	49	97	98	84	27	60
11	M	2.345±.005	2.266±.006	2.257±.005	2.172±.007	2.257±.004	2.274±.004	2.293±.005	2.220±.007	2.260±.005
	C	2.93±.15	3.24±.18	3.12±.15	3.27±.22	2.61±.13	3.52±.12	2.99±.16	2.31±.21	2.50±.15
	N			99	29	97	98	84	27	60
26:11	M			77.74±.91	49.50±.91	35.90±.76	31.62±.70	22.32±.59	58.52±1.82	26.40±.73
	C			17.34	20.10	11.14	32.55	35.68	24.02	31.76
	N			99	49	97	98	84	27	60

absolutely and relatively narrow wings. The black American bees have to be placed not far from the type of the Ukrainian bees in respect to the characters of the wing, having even a shorter distal length.

Table 20 contains data on variation of the hind legs. The absolute size of the leg joints of American Italians is smaller than in Middle Russian bees (for the difference in the first joint of the tarsus the probable error ratio is only 3.8). In respect to the absolute and relative size of the leg joints the American Italians practically agree with the Ukrainian bees. In harmony with a larger size of wings the American Italians have also longer joints of the hind legs than the Italians from Italian queens. The latter are definitely more long legged (according to the indices) than the American Italian bees.

The biometrical constants and the results of comparison of different races in respect to the characters measured on the abdomen are represented in Table 21.

The American Italians compared with Middle Russian bees show that all abdominal characteristics are smaller in size in the former group. The American Italians have practically the same size of abdomen as the Ukrainian bees, being therefore larger than Italian bees from Italy. In regard to the index of the wax gland the American Italians correspond perfectly to the Ukrainian bees, being just between the Middle Russian and Italians from Italy.

Concerning the coloration of the third band of the abdomen the yellow band is definitely larger in the American Italians than in the Italians from Italy. The scheme of coloration in figure 14 shows that, among the bees studied, the American Italians represent the lightest colored type of bees. It is evident that this is the result of an artificial selection in the direction of the production of light colored golden bees.

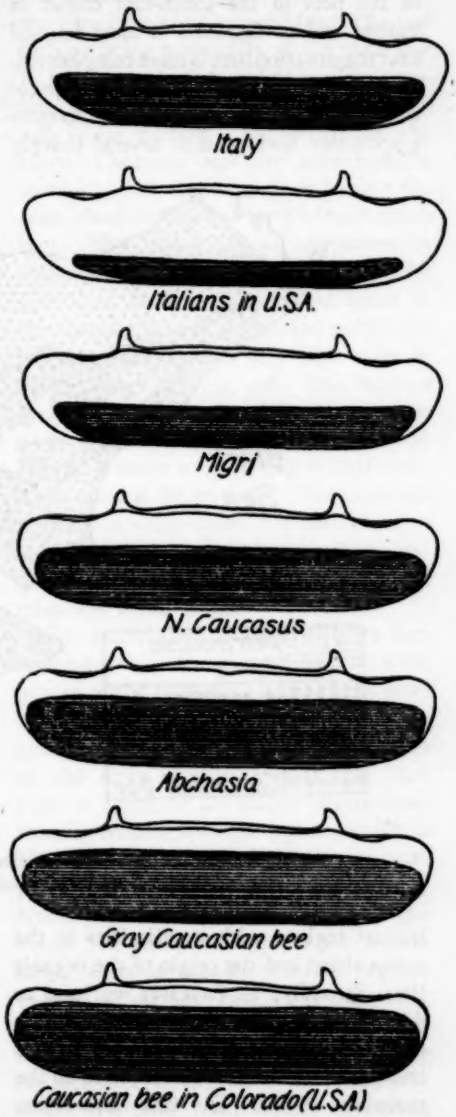


FIG. 14. SCHEME OF COLORATION OF THE THIRD TERGUM OF ITALIAN AND CAUCASIAN BEES BASED ON ACTUAL AVERAGE MEASUREMENTS OF THE YELLOW STRIPE

CAUCASIAN BEE RACES

Turning our attention to the variation of the bees in the south-east corner of Europe and in Caucasus it must be said that the situation here is more complicated. This is due to two probable groups of causes. First, the Caucasus is zoogeographically divided into several sharply limited regions with peculiarities in the composition and the origin of the organic life. Secondly, in Caucasus we have to deal not only with a change of climatic conditions on the plain but also with a change which occurs with elevation on the mountain chains. The first observation of the differentiation of the Caucasian bees in groups has been made in regard to the coloration of the abdomen.

According to Gorbatschev (see the map in Fig. 15 taken from his article, (26)) the Central chain of the Caucasian mountains is populated by gray Caucasian bees, which he describes under the name of *Apis mellifera caucasica* Gorbatschev.

Another distinct form is the so-called yellow Persian bee inhabiting Lenkoran and some regions of Armenia and Azerbeijan. The northern Caucasus prairies and the hills in Transcaucasia are populated by a bee of an intermediate type—hybrids according to Gorbatschev's interpretation. We combined our material from Caucasus in groups according to the origin, i.e., locality. In our article on hooks (11) we included the bees from Migri representing true yellow Persian bees in the

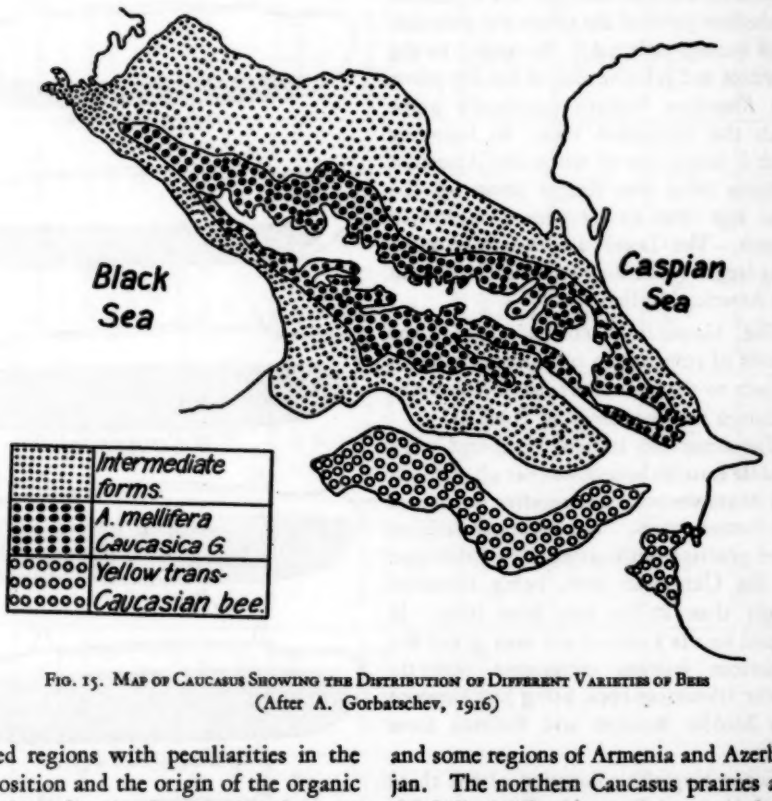


FIG. 15. MAP OF CAUCASUS SHOWING THE DISTRIBUTION OF DIFFERENT VARIETIES OF BEES (After A. Gorbatschev, 1916)

same group with those from Delijan which are according to our later investigation on coloration quite different from them, being very close to gray Caucasian bees. Bees from Tiflis, Swanetia and Kutais we consider as true *Apis mellifera caucasica* Gorbatschev. The bees from apiaries on the eastern coast of the Black Sea (see our map, Fig. 9) we shall treat separately, being informed that the bees from this region (Abchasia and adjacent localities) differ from the gray Caucasian bees of the Central chain in respect to different peculiarities of their behavior and biology. Bees sent to us from Stavropol and Maikop have been specified as North Caucasian bees, although the Maikop bees are, it seems, a link between these and Mountain gray bees. We had also the opportunity to investigate Caucasian bees cultivated in the United States in Colorado.

In Table 22 are presented data from different sources relating to the tongue length of Caucasian bees. The largest material comes from Tiflis, where a state apiary has been selling queens of the Caucasian gray bee for many years. The apiary was under the supervision of K. A. Gorbatschev. It seems that the length of the tongue of Tiflis and Abchasian bees (Gagri, Adler, Kichmai) lies between the limits of 6.60 and 6.70 millimeters. An insufficient number of colonies or a lack of proper precautions in collecting the material does not allow us to draw any definite conclusion about the deviation of other Caucasian bees from gray ones. The North and Transcaucasian bees must have an average tongue length in no case below 6.500 millimeters. Further investigation will be necessary to clear up this question.

Turning our attention to other characters we see that both wing lengths show that the Caucasian bees are smaller than Middle Russian ones. Compared with Ukrainians we see that only North Caucasus, Abchasian, and Migri bees show statistically significant differences, the bees from the Central Mountains and Delijan being practically of the same size in both lengths (24 and 25). The absolute width of the wing does not give a very clear picture. The wings of the North Caucasus bees are exceptionally narrow, other Caucasian bees having the same absolute width as the Middle Russian bees. The index 25:24 continues a decrease southwards which was begun by Ukrainian bees, then increases again in Abchasian, Central Mountains and Delidjan bees and reaches a very high value in Migri bees, $94.81 \pm .28$. The relative width of the wings is, with the exception of North Caucasian bees, higher than in Middle Russian ones, having an extremely high value in Migri bees. The Colorado bees are in their coloration very close to the gray Caucasian mountain bees and differ from them only in absolutely and relatively broad wings.

The absolute size of the tarsal joint does not give a very clear picture, being in some groups of the Caucasian bees smaller than in Middle Russian ones and in others practically equal to them. The variation of the tibia is quite remarkable. This joint is *larger*, in all except Migri bees, than in Middle Russian and naturally in Ukrainian bees. The femur is, as compared with Middle Russian bees, larger in North Caucasus and smaller in Migri bees. The relative length of the legs is larger than in Middle Russian bees as shown by all the indices. Particularly pronounced is the difference in the relative length of the femur. The ratios showing the statistical differences of the proportion of the first tarsal joint are not significant in the cases of Abchasian and Caucasus Mountain bees. The Colorado Caucasians have absolutely longer tarsal joints than

TABLE 22

Tongue length of Caucasian worker bees from different localities (Data collected from different sources)

ORIGIN OF THE MATERIAL OR RACE	PLACE OF DEVELOPMENT	NUMBER OF COLONIES	NUMBER OF SPECIMENS	MEAN	COEFFICIENT OF VARIATION	HOW COLLECTED	AUTHOR
Gagri (Abchasia).....	Orel district (Middle Russia)	3	300	6.731±.007	2.64	Boiling water, etc.	Chocklov, 1918
Kars (W. Transcaucasia).....	Orel district (Middle Russia)	3	300	6.642±.005	2.02	Boiling water, etc.	Chocklov, 1918
Tiflis.....	Tiflis	3	150	6.602		Collected in boiling water and sent in 2% formalin	Michailov, 1917
Tiflis.....	Nizhni Novgorod	4	379	6.670±.004	1.71±.04	Boiling water	Kurotschkin, 1918
Tiflis.....	Tiflis	5	154	6.658±.006		Boiling water, etc.	Michailov, 1918
Kuban (N. Caucasus).....	Kuban	3	50	6.531±.013		Boiling water, etc.	Michailov, 1916
Kichmai (Sotchi-Tuapse W. Caucasus)..	Kichmai	10	39	6.621±.016		Tongue carefully stretched out	Alpatov, 1928
Adler (W. Caucasus).....	Adler	13	58	6.653±.010		Preserved in dry condition	Alpatov, 1928
Gray Caucasian bee.....	Colorado (U. S. A.)	10	circ. 50	6.638±.009		Boiling water, etc.	Alpatov, 1928
Maikop (N. Caucasus).....	Maikop	more than 8	19	6.539±.031		Collected dry without any precautions	Alpatov, 1928
Delidjan (Transcaucasus).....	Delidjan	4	29	6.509±.020		Collected dry without any precautions	Alpatov, 1928
Migri (Transcaucasus).....	Migri	3	13	6.511±.020		Collected dry without any precautions	Alpatov, 1928

Abchasian, absolutely larger tibia than Caucasus Mountain bees, and shorter femur than dark bees from Caucasus. The indices in Colorado Caucasians show very high values, even in more pronounced form than in dark bees from Caucasus.

Examining the characters on the abdomen we can establish two rules: the first is that all Caucasian bees are smaller than the Middle Russian. Some of them are smaller than the Ukrainian, while some are practically equal in size to the latter. Only the 10th and 8th measurements are exceptions to the following serial change in abdomen measurements: North Caucasus < Abchasia < Central Mountains > Migri.

The proportions of the wax sternum show in general that the Caucasian bees have a smaller wax gland than the Middle Russian; the relationship of Caucasian bees is as follows: North Caucasus < Abchasia < Caucasus Mountains = Migri.

The Caucasians from Colorado are near the Abchasian bees in respect of the abdominal measurements, being in some of them a little smaller than the gray Caucasian bees from Caucasus.

The coloration of Caucasian bees presents no difficulties in interpretation. The gray Caucasian bees from the Caucasus Mountain chain are the darkest, the opposite end of the series being occupied by Migri bees. The Colorado Caucasians do not differ significantly from those of the Caucasus Mountains. The Abchasian and North Caucasian bees are closely related, having a large percentage of yellow color on the third tergum.

The last relationship that we have to discuss is that of yellow Caucasian bees to Italians. We shall compare them only with Italians bred in Italy and from queens imported from Italy. It seems very probable that the tongue length of North Caucasian and Migri bees is greater than that of Italian bees. The Italians, judging from the whole experience, have a tongue length varying in different apiaries from 6.15 to 6.45. The North Caucasian bees have an average tongue length at least not less than 6.50 millimeters. The North Caucasian bees are larger than the Italians in regard to all the absolute measurements. There is a pronounced difference between them in that the Caucasian bees have a narrower form of the wing (2:24). The Italians have relatively large first joints and short tibias. The coloration of the third tergum is much lighter. The Migri bees have also nearly all absolute measurements larger than those of the Italian bees (exceptions are the following characters: 24 where $R = 2.9$, 5 where $R = 3.3$, and 23 where $R = 2.0$). The coloration of Migri bees is even lighter than that of the bees from Italy. Wings have a high value of the indices 2:24 and 25:24. The relative length of the first tarsal joint is larger in Italian than in Migri bees. Both groups of Caucasian bees have a larger wax gland index than the Italians ($R = 4.4$ and 8.7). It seems that both groups of yellow Caucasian bees differing from the Italians have some peculiarities linking them with other Caucasian bees (longer tongue, larger size of the body and of the wing). The definite conclusion is that the Caucasian yellow bees have to be considered as a strain of southern bees independent of the yellow Italian bees—*Apis mellifera ligustica* Spinola.

HEREDITARY CHARACTER OF RACIAL DIFFERENCES IN BEES

The racial differences which have been described above as occurring in bees belonging to different parts of the area of distribution of species of *Apis mellifera* L. raise the question of their hereditary

nature. Unfortunately nothing is known about the heredity of the honey bee. This is due to the difficulties of controlling the mating of the queens, which takes place in the air. Up to the present time all the attempts to mate the queen indoors have failed. Quite recently Watson (80, 81) developed a very delicate technique for the instrumental insemination of the queen. Without doubt this method will help very much to investigate thoroughly the genetics of one of our domesticated animals.

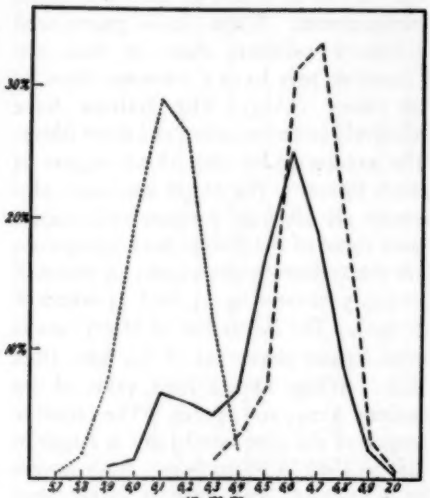


FIG. 16. VARIATION CURVES OF THE TONGUE LENGTH OF GRAY CAUCASIAN BEES REARED IN MIDDLE RUSSIA AS COMPARED WITH MOSCOW BEES (DOTTED LINE)

Continuous line represents the variation of worker bees collected from nine colonies where the Moscow queens were replaced by gray Caucasian queens. The dash line shows the variation of bees from four colonies of gray Caucasian bees cultivated in Nizhni Nowgorod. The frequencies have been calculated in percents.

We propose now to bring together a few of the facts relating to the inheritance of racial differences in the honey bee. One of the oldest facts is the observation of Dzierzon of the transmission of color in a cross of the black and the yellow Italian bees. These observations gave origin to the discovery of the parthenogenetic nature of the drones. A recent publication of Newell (59) shows that the color is inherited as a Mendelian character. Besides that, the stability of the racial differences in color has been proved hundreds of times in observations of the progeny of the queens of yellow races imported to the north. From this point of view the transportation of different strains of the honey bee to the United States represents in itself a great experiment. The differences found by us between the yellow and the black bees in the United States, which are of the same sense and direction as the differences between the Northern and Southern European bees, furnish a direct proof of the stability of these racial characteristics. The same is true of the Caucasians cultivated in the United States of America. We have seen that in their constitutional characteristics they remain extremely closely related to the ancestral stock. Through the courtesy of A. F. Gubin, Director of the Moscow Apicultural Experiment Station, we possess some data illustrating the inheritance of the tongue length of Caucasian bees in Middle Russia. Figure 16 represents variation curves of the native Moscow bees (dotted line) and bees produced by gray Caucasian queens introduced into Moscow colonies (continuous line). The Moscow curve is based on measurements of 1000 bees taken from ten colonies, the Caucasians on measurements of 900 bees from nine colonies. The bees were measured a few weeks after the requeening of the Moscow colonies (nine) by Caucasian queens. Not all the Moscow worker bees had been replaced by workers emerged from the brood of Caucasian queens; the left summit in the Caucasian curves represents the

remaining Moscow bees. The dash line shows the variation curve of four colonies of Gray Caucasian bees produced by Caucasian (Tiflis) queens sent to Nizhni Novgorod (Middle Russia). We can see that the progeny of Caucasian bees developed in Middle Russia has approximately the same length of tongue as the Caucasian gray Mountain bees (6.60–6.70 mm.). Another example is a transportation of four colonies of bees from the Kursk district to Moscow. Measuring the tongue length of three Moscow colonies and of the colonies brought the year before from Kursk (let us call them Ukrainians), we get the following average length of tongue for the two groups under consideration: Moscow 6.038 ± .016, Kursk 6.321 ± .010, Diff. = .283 ± .018, Ratio = 15.7. Kursk is situated 4° south of Moscow and according to our formula we should expect there bees with a tongue length 0.302 mm. longer than in Moscow. This figure is not far from the difference obtained above. Figure 17 shows the curves of the bees of Kursk and native Moscow ones. Measurements of other characters showed a slight approach of the Ukrainian bee to the type of Ukrainian bee established above—smaller size of body, of the wings, and of the legs, and a larger number of hooks. But owing to the small number of cases, the large probable errors do not permit us to affirm positively that Ukrainian bees transported to the North preserve a southern constitutional type. This is one of the most important problems to be further investigated in the future.

We cannot omit to mention a paper of Michailov (53) in which the author attempts to compare the offspring of the Caucasian queens developed in Tiflis (Caucasus) and in Tula (Middle Russia). Queens which had already wintered once were sent from Tiflis to Tula and introduced there into hives with brood and not field bees. Special care was taken to send the queens accompanied by their own offspring, which were used to characterize the Caucasian bees born in Caucasus. In two months after the arrival of Caucasian queens a collection of bees from their hive was made. The bees were collected during their emergence so that it is safe to say that they represent the offspring of the Caucasian queens. In this way offspring

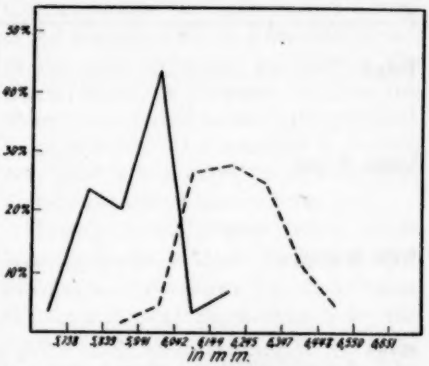


FIG. 17. VARIATION CURVES OF THE TONGUE LENGTH OF NATIVE MOSCOW BEES AND BEES FROM COLONIES TRANSPORTED TO MOSCOW FROM THE SOUTH

The continuous line represents bees taken from three colonies of native Moscow bees. The dotted line is based on measurements of bees from four colonies which one year before were transported to Moscow from a southern locality (Kursk District). The frequencies are expressed as percents.

of five queens has been investigated. Table 23 represents the absolute measurements and they confirm the conclusion reached above regarding the north-south variation in the constitution of the bee body.

The range of variation of the tongue index is from 126.7 to 129.0 for bees on the plain of European Russia (Leningrad, Tula). For the Caucasian bees this index has a quite different range, namely 145–148. The wing index for Russian bees is less than 200, for Caucasian bees it is

above 200. The wings are broader in Caucasian bees. The Caucasian bees born in Tula remain within the limits characteristic of Caucasian bees in regard to the proportions of the body. The reduction of the tongue and wing measurements in Tula offspring of the Caucasian bees is not in accord with the observations of Chochlov, Kurotchkin, Gubin and our own measurements. It seems to us that the only probable explanation is that in Michailov's case the queens were introduced not in normal colonies but in hives with young brood and young bees. We have seen above that there is a certain influence of the age of the nurse bees on the reduction of the bee body in size. In both cases the strength and the normal composition of the bee colony were disturbed, which had as a consequence a

TABLE 23

Biometrical constants of Caucasian worker bees born in Tiflis compared with their sisters produced by the same mothers shipped to Middle Russia (Tula)

(From Michailov, 1928)

	154 BEES FROM 5 COLONIES: BORN IN TIFLIS	DIFFERENCE AND $R = \frac{\text{DIFF.}}{\text{P.E.}}$	490 BEES FROM THE SAME QUEENS: BORN IN TULA
Tongue	6.658±.005	.166±.008	6.492±.005
	1.61 ±.06	R = 20.7	2.78 ±.06
Length of wing	9.226±.008	.076±.009	9.150±.004
	1.57 ±.06	R = 8.4	1.60 ±.03
Width of wing	3.153±.004	.030±.004	3.123±.001
	2.31 ±.09	R = 7.5	2.39 ±.05
Hooks	21.73 ±.11	.47 ±.12	21.26±.06
	9.52 ±.37	R = 3.9	8.60 ±.19
Tergum (III + IV)	4.461±.006	.024±.008	4.485±.005
	2.34 ±.09	R = 3.0	3.70 ±.08
Tongue: tergum (III + IV)	149.32 ±.21	4.39 ±.28	144.93±.19
	2.65 ±.10	R = 15.7	4.31 ±.09
Length of wing: tergum (III + IV)	206.91 ±.29	2.64 ±.37	204.27 ±.23
	2.54 ±.10	R = 7.1	3.72 ±.08
Width of wing: length of wing	34.18 ±.03	.27 ±.04	33.91 ±.01
	1.87 ±.07	R = 6.75	1.93 ±.04

decrease in size of different parts of the body of the bees, although in the first and in the second case different parts of the body were not influenced in an identical way.

In any case the whole bulk of the material on the transportation of bee races to new localities shows that the characteristics are inherited. They cannot be considered as purely phenotypical phenomena.

BIOLOGICAL DIFFERENCES OF BEE RACES

It is beyond the plan of the present paper to bring together the tremendous number of observations scattered through the beekeeping literature of every country in the world concerning the racial differences in the behavior and productiveness of the honey bee. The most important defect in all such results is that they are usually based on the observation of a comparatively restricted number of cases. We have shown above that a bee colony can be very easily described by a number of physical characteristics. The same is true in respect to the biological characteristics. This fact is known to everybody who has occasion to handle bees. This highly developed individuality of bee colonies prevents us from drawing conclusions about racial differences unless a large number of colonies of races under comparison are examined. As a rule this is rarely fulfilled. In many cases of racial description we are doubtful as to whether the observed differences are to be considered as real differences between the races under comparison, or as chance deviations of a few colonies with imported queens from the colonies with native bees. The second point is that the racial differences in biological characteristics as well as in morphological ones are usually of a quantitative character, the variation being transgressive. Consequently it is highly desirable to have a numerical expression of the biological characteristics. Unfortunately at the present time methods for quantitative observations of bee behavior are almost entirely wanting. The only attempt to use exact measurements in characterizing one of the most important features of comparative queen biology has been made by Nolan (60) in his brood rearing investigations.

It seems to us that at the present time the comparative and quantitative survey of the biology of different bee races is one of the most important questions in the natural history of the honey bee, from the theoretical as well as from the practical point of view. Our intention is to give here only a few examples of biological differences between races of bees.

On the plain of European Russia, which is occupied by a black variety of *Apis mellifera*, we have shown a gradual change in morphological characteristics in the southern direction. This is accompanied by some changes in swarm instinct. The first (or prime) swarm is a group of bees leaving the colony with the old queen after the sealing of the queen cells. For the Middle Russian bee (Briuchanenko, 21) and the German bee (Zander, 84) that event takes place on the same day or on the next day after the sealing of the first queen cell. In the Ukrainian bee (Southern Russia) this happens only on the third day and for the Crimean bees (farther south) the bees do not swarm before the sixth to eighth day.

Among the Ukrainian bees cases of occurrence of two queens in one hive have been reported oftener than among the Middle Russians. For North Caucasian bees, according to the observation of beekeepers, sometimes thirty per cent of the colonies have two queens who are

peacefully living together, a picture which is unfamiliar to a beekeeper in northern and southern Russia.

The number of after swarms produced in different races is very variable. A. I. and E. R. Root (69) write evidently about the Italian bee cultivated in the United States of America: "All swarms that come out after the first swarm, or are led by a virgin queen or a plurality of them are generally termed after-swarms; and all swarms after the first are accompanied by such queens. There may be from one all the way up to a half dozen swarms." Nearly the same limit of the number of swarms is usually indicated for the Middle Russian bee. The yellow Caucasian bees according to Gorbatschev (26) are excessive swarmers, having sometimes twelve swarms per colony. On the other hand the gray mountain bees have a lower swarm instinct, approaching in that respect the bees from northern localities. A. and E. Root in their book (69) do not make any distinction between the yellow and gray bees from Caucasus. They write (*loc. cit.*, p. 715) about Caucasians in general. The most serious objection to them is their propensity to swarm. It is even more pronounced than in Carniolans.

Peculiarities in the development of the swarming instinct may characterize races of bees of a very limited territory. It has been reported that the bees of the Lüneburg marches in Germany are extreme swarmers. On account of this peculiarity they have been described under a special name as *A. mellifera Lehzeni* Buttel-Reepen (Buttel-Reepen, 20). An interesting characteristic of the Caucasian bee is a very high number of natural queen cells. The Middle European bee has, according to Berlepsch, 5–20 queen cells. The first exact number given by Koshevnikov (33) was 150 cells in a colony. Pickel recently indicated that the North Caucasian-Kuban bees have sometimes as many as 350 queen cells. Mosolevsky (58) reports that the Abchasian bees build very few queen cells, differing in that respect from the other Caucasian bees. In regard to the number of queen cells the Caucasian bee approaches the Egyptians (100–200 queen cells according to Buttel-Reepen) and Syrians (200–300 cells according to the same authority). Another peculiarity related to the reproductive functions which is developed in different degrees among races of the honey bee is the occurrence of egg laying worker bees (Koshevnikov, 33). Postojalko (67) indicated that the yellow Caucasian bees have more often egg-laying worker bees than the gray ones.

Turning our attention to the problem of differences of the bees belonging to different races in regard to their ability to collect nectar from different flowers, it may be pointed out that this particular question was just the starting point of the whole biometrical work on bee races. In the beginning of this century the Root Company claimed that its bees are able to collect nectar from the red clover—a plant which is not frequently visited by bees. The same question shortly before the world war was a subject of intensive investigation in Russia on the estates of one of the members of the royal family. I. N. Klingen (32), a broad minded agronomist, was the leader of these investigations and their practical application. He claimed to prove that the visiting of the red clover by bees depends on two circumstances: (1) the absence at the moment of the blooming of the red clover of any competition with other nectar secreting plants, (2) cultivation of long tongued bees (in his case Caucasian). Klingen was an ardent amateur of the gray Caucasian bees and several

hundreds of Caucasian colonies were cultivated under his direction on the estates mentioned. His data show, with perfect evidence, that in the case where the clover was provided with a certain number of hives of Caucasian bees the crop of clover seed was much higher than in the case where these bees were absent.

The same question arose recently in Russia and became a subject of detailed investigation of several Apicultural Experimental Stations. We have the pleasure to acknowledge the permission of A. F. Gubin, Director of the Moscow Apicultural Experiment Station to publish the data obtained by him concerning the specific qualities of Middle Russian and Gray Caucasian bees. In the beginning of the summer of the year 1926 in nine colonies of the Moscow black native bees the queens were replaced by queens of the gray Caucasian bee sent from Tiflis (Caucasus). When the newly emerged Caucasian bees replaced nearly completely the Russian bees (see Fig. 16), samples of 100 bees were taken from these nine colonies as well as from ten other colonies with replaced Moscow queens. The variation curve for 1900 bees is represented on figure 18 by the continuous line. It is clear that the bimodal character of the curve is due to the presence of long tongued Caucasian worker bees with an average tongue length of about 6.60 mm. At the same time on the field of clover situated near to the apiary a collection of bees visiting the clover was made. The dotted line in Fig. 17 represents the variability of bees collected on red clover. Like the continuous line the dotted curve shows two peaks, one corresponding to the Moscow bees and the other to the Gray Caucasians. The most interesting fact is that in the dotted line the peak which represents the Middle Russian bees working on red clover is shifted a little to the right from the peak of Middle Russian bees collected from hives. It means that the Middle Russian bees which were collected during their work on red clover have a longer tongue than the general population of Middle Russian (Moscow) bees. In other words only comparatively long tongued bees are able to work on clover. The peak for Caucasian bees collected on clover does not show any shifting along the horizontal axis. This indicated that in the case of the Caucasians a selection of long tongued individuals did not occur. All Caucasian bees could work equally on red clover. We considered this discovery of A. F. Gubin as one of the most interesting facts concerning the relationship between the honey bee and flowers.

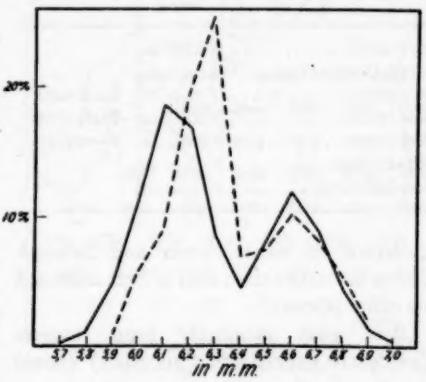


FIG. 18. FREQUENCY DISTRIBUTIONS OF TONGUE LENGTHS OF BEES

The continuous curve shows the variation of the tongue length of 1900 bees taken from nineteen hives of the apiary of the Department of Apiculture of the Moscow District Agricultural Experimental Station. In 9 of these hives the Moscow native queens have been replaced by queens of the gray Caucasian race. The dashed curve represents the variation of 228 bees collected near to the apiary on flowers of red clover. The curves are based on data obtained through the courtesy of Dr. A. F. Gubin, Director of the Department of Apiculture.

Quite recently several attempts have been made to study the tongue length of

bees collected from other honey plants. Table 24 presents data published by Gubin (29). It can be seen that the average length of the tongue of the bees collected on white clover and Swedish clover is smaller than that of bees collected on other plants.

TABLE 24

Average length of the tongue of the bees collected on different nectar producing flowers

(From Gubin, A. F., 1928)

	MEAN AND MEAN ERROR	
Fire weed	6.24±.01	
Vetch (*Vicia villosa*)	6.52±.01	
Red clover	6.22±.01	Rare visits
Red clover	6.22±.02	Mass visits
Red clover	6.30±.02	Mass visits
White clover	6.12±.01	
Swedish clover	6.14±.01	

Bees with extremely long tongues (evidently exclusively Caucasian) visited the vetch, while on the red clover there were working also Middle Russian bees, which lowered the average value of tongue length of the bees collected from this plant.

In Table 25 are represented analogous data collected by A. Kurotchkin in Nizhni Nowgorod. The apiary of the Nizhni Nowgorod Zootechnical Experimental Station contained, besides native bees, also several colonies of Caucasian bees from Tiflis. Gubin's and Kurotchkin's data are not comparable. The conditions of honey secretion in two different localities and different seasons of the year are so variable that at the present moment we are not able to draw very definite conclusions about the absolute requirements in tongue length necessary for work on such a plant as red clover. It is not apparent why the bees on red clover in Kurotchkin's measurements have such a short tongue as compared with the measurements of Gubin. In Table 25 the most striking fact is the highest value for the late *Phacelia* which evidently attracted mostly Caucasian bees. Another interesting point observed by Kurotchkin is that the bees collecting pollen show a pronounced difference in the length of the tongue from those collecting nectar. It means that among the bees engaged in pollen collecting the native short tongued individuals played a significant rôle, while they were absent among bees sucking nectar.

TABLE 25

Average length of the tongue of the bees collected on different nectar producing flowers

(From Kurotchkin, 1928)

	MEAN AND MEAN ERROR	TIME OF DAY	DATE	NO. OF SPECIMENS
Red clover	6.09±.02		23.7	36
Buckwheat	6.09±.02		1.8	46
Early Phacelia	6.20±.02		20.7	95
Late Phacelia	6.60±.02	6–7 a.m.	23.8	124
Late Phacelia	6.53±.02	7–8 a.m.	23.8	95
Late Phacelia	6.59±.02		23.8	50
Late Phacelia (bees with pollen mass)	6.35±.02		27.8	76
Late Phacelia (bees without pollen mass)	6.52±.02		27.8	89
Echum vulgare	6.14±.01		5.7	100

Meager as the existing data are, they show a promising possibility for a systematic investigation of the selection and adaptation of the worker bees of different races to different plants. The preference of certain bee races for certain plants is the cause of differences in the quality of honey collected. It happens often that the color and flavor of the honey collected in the same locality by colonies belonging to different races differ greatly. This has naturally a certain importance from the point of view of the marketing of honey.

Another racial characteristic of commercial importance is the capping of the combs. Phillips (65) gives the following description of this phenomenon: "Some races of bees fill their honey combs more completely than others and when the honey is in contact with capping it gives the honey the appearance that is described as watery. When the capping is separated from the honey by an air space the capping appears white (or yellow, depending on the color of the wax). In general the black races seem to produce whiter comb capping than the yellow bees."

A long series of different characteristics of high economic importance has been attributed to different races. We cannot go into details of this part of the problem, especially because these characteristics have not yet been expressed in numerical form. According to the experience of American beekeepers "an important characteristic of Italians is the resistance to European foulbrood. In that respect they have been compared chiefly with German bees to which race they are vastly superior" (Phillips, 65, p. 211). The Caucasians are, so far as we know, the most gentle bees in the world.

Numerous observations have been published concerning the racial differences in productiveness. We believe that a scientific, statistically controlled contest, including the most important races, would be a very important enterprise for theoretical as well as practical conclusions.

TAXONOMICAL CONCLUSIONS AS BASED ON BIOMETRICAL DATA

In one of our papers (1) we expressed the opinion that the classification of the

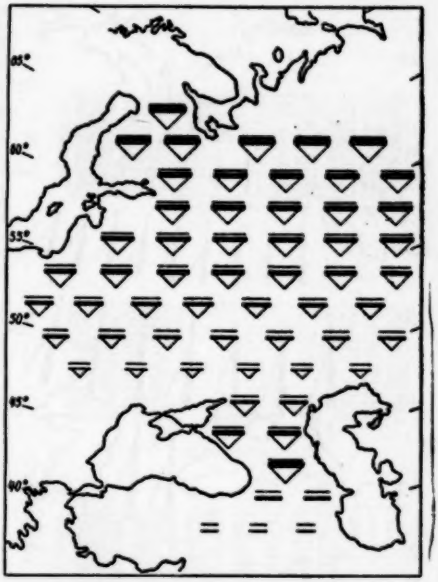


FIG. 19. DIAGRAMMATIC MAP OF EUROPEAN RUSSIA
The size of each group of signs represents the size of the bees. The width of the middle bar corresponds to the coloration of the abdomen. The relative size of V-shaped sign represents the relative size of the wax gland surfaces. Owing to the lack of space North Caucasus is covered with signs corresponding to a more northern or mountain type of bee.

taxonomic categories below the rank of species ought to be made only on the basis of a detailed and thorough investigation of the geographical variation of a given species. An investigation of this kind, based on *Apis mellifera* L. as material, has been described in this paper. Our purpose now is to discuss the bearing of the results on taxonomy as well as on

problems of variation in general. Our experience concerning the Russian plain and the Caucasus is generalized on the schematic maps represented in figures 19 and 20. The first map (Fig. 19) shows graphically the gradual change in body size, color, and relative size of the wax glands, while the absolute length of tongue and the relative length of the hind legs is shown on figure 20. As far as the Russian plain is concerned both maps show a harmonized change of characters from the north to the south. But when we start to consider Caucasus a pronounced difference appears between groups of characters represented on the two maps. The size of the body, coloration and relative size of the wax gland show, in the gray Caucasian mountain bee, a restoration of a picture existing in Middle Russia (i.e., far in the North), while the size of the tongue and the relative length of the hind legs show a continuous uninterrupted change southwards. Each of these two groups of measurements taken separately gives a splendid example of the gradual continuous geographical variation of two complexes of characters. It is perfectly clear that in the honey bees, at least in the area covered by our survey, the absolute size of the body (and of the wings), the relative size of the wax gland and the color of the abdomen are linked together and vary as a system. The same is true concerning the length of the tongue and the relative length of the hind legs. On the plain the two groups of characteristics are closely linked together but by a negative correlation. The situation is completely different in the Caucasus Mountains. Here the negative correlations disappear and we observe a complete independence in the variation of racial characteristics. Sumner (75) pointed out that the "existence of a correlation between two characters in the individual is not, in itself, sufficient to insure a constant correlation, geographically speaking." Our case brings evidence that the law of individual variation has a perfect analogy in group variation. Just as in the variations within the limit of a race we have correlative (negative and positive) variation, so the variation of group characters follows the same laws. It seems that we are justified in formulating two laws of geographical variation in the honey bee: (1) the variation is continuous and gradual, and (2) the characters of geographical forms may be correlated (positively and negatively) or may vary independently from each other. These two rules of the relationship of measurable

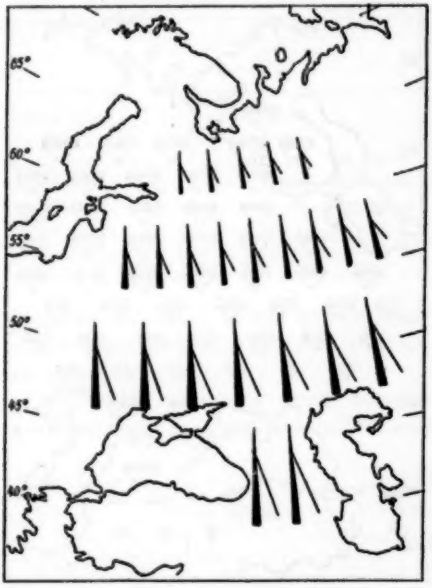


FIG. 20. DIAGRAMMATIC MAP OF EUROPEAN RUSSIA

The vertical bars with broader basis represent the tongue length. The lines attached to the right side of the bars show the proportion of legs to body size.

characteristics in the honey bee are very similar to the situation observed by Sumner in *Peromyscus* (75).

Before comparing in more detail the geographical variation of the honey bees with that of other animals we must connect our finding with the requirements of taxonomy. The first question concerns the reconciling of the usual methods of taxonomical description of lower taxonomical groups with the fact of the existence of a continuous geographical variation. One of the most definite determinations of a subspecies or geographical race was given by Semenov Tian-Schansky (73). It is as follows:

(1) Presence of one or several hereditary characteristics.
(2) Relative stability of these characteristics.
(3) Occurrence of intermediate forms linking two subspecific forms together in the area between the areas of distribution of the forms under consideration.
(4) A definite area of distribution.
(5) Psycho-physical isolation between the races being in the primitive stages of its development makes quite possible the production of a fertile progeny in inter-racial crosses.

Following this conception we feel justified in giving a special name to each local race of the honey bee inhabiting the plain of European Russia because each of them carries the peculiarities of a true geographical race. Increasing the number of points from which our material is taken we may increase unlimitedly the number of the races and each of them would require a special name. Sumner (74) has emphasized the importance of sections across the area of distribution "of a certain species by running a series of trapping stations through the territory of two adjacent subspecies at right angles to the supposed line of demarcation." He has also given two schemes of the interrelationships of subspecies which have a certain analogy with the scheme of Semenov Tian-Schansky (73) and our own proposed in the present paper.

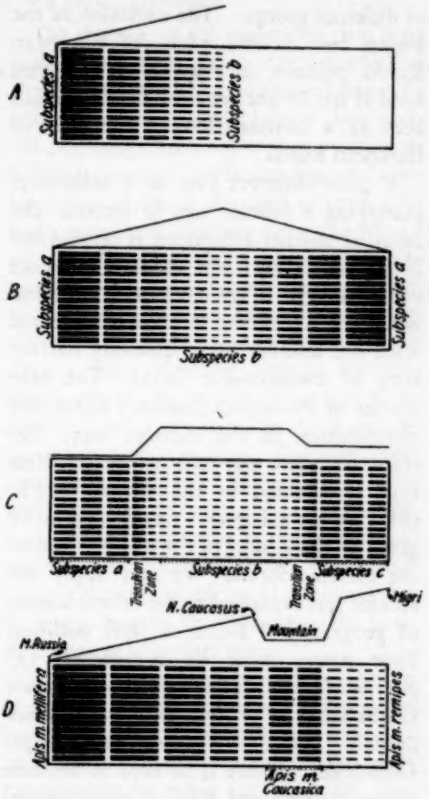


FIG. 21. DIAGRAMS REPRESENTING DIFFERENT TYPES OF GEOGRAPHICAL VARIATION

A. Gradual continuous variation.
B. Local form (*b*) surrounded by another (*a*) through a continuous chain of intergrades.
C. Local form (*b*), uniform in a certain area, connected with two others (*a* and *c*) by a comparatively narrow zone of intergrades.
D. Scheme of the north-south variation of the honey bee in Eastern Europe and Caucasus based on size of body, coloration and relative wax gland surface.

In figure 21 such a case is represented by diagram *A*. Some time ago in our papers on Russian Arctic Decapoda (1) we proposed to give subspecific names in cases of gradual geographical variation to extreme

members of the geographical chain of forms. Examples of this first type of subspeciation are known to taxonomists of different groups. The variation of the honey bee on the plain of European Russia presents an example of just this kind if we do not consider the Caucasian bees as a continuation of the bees in European Russia.

A quite different case of a subspecies occupying a definite area in between the areas of another subspecies is represented in scheme *C* (Fig. 21). This is the most common type of geographical variation when the subspecific forms are connected with one another by a relatively narrow zone of transgressive forms. The subspecies of *Peromyscus* (Sumner) show this phenomenon in the clearest way. Besides that there may exist an intermediate type represented in the scheme *B*. In this case the subspecific names have to be given to the climax of the changes and to the extreme forms. We may apply the scheme just explained to the denomination of geographical forms of *Apis mellifera*. Four names must be considered: (1) *Apis mellifera* L., (2) *Apis mellifera caucasica* Gorbatschev, (3) *Apis mellifera ligustica* Spinola, and (4) *Apis mellifera remipes* Gerstäcker. There is no need to hesitate about the first and third of these names. They refer to the black European and Italian yellow varieties of the honey bee.

The taxonomy of the Caucasian bees has been far from clear. The west European taxonomists (Buttel-Reepen, Zander, 20, 83) identified all the Caucasian bees as *Apis mellifera remipes*, including in this conception yellow as well as gray Caucasian bees. A. N. Gorbatschev in 1916 recognized the independence of the gray mountain Caucasian bees from the yellow Caucasian bees, basing his conclusion on peculiarities of coloration, behavior, biology and specific area of distribution. He gave to the gray Caucasian bee the name *Apis mellifera caucasica* Gorbatschev. The origin of the name *Apis remipes* is as follows. This name is derived from a specimen of the honey bee belonging to the famous Russian zoologist Pallas, who recognized the specificity of Caucasian bees of the yellow type and described this form in one of his unpublished manuscripts. The specimen with the original label is preserved in the Berlin Zoological Museum and was mentioned in a few words by Gerstäcker (see Buttel-Reepen, 20). According to the rules of zoological nomenclature we have to consider Gerstäcker as the author of this form because Pallas never printed a single word concerning it. The question to solve is whether Pallas's description is of the gray mountain bee or of the yellow one. Koschevnikov (33) has expressed the opinion that the *Apis remipes* Pallas is identical with the Italian bees, in other words belongs to the yellow type. Gerstäcker in mentioning Pallas's specimen indicates that the bee was provided with yellow bands on the abdomen. The author of the present paper was able, thanks to the courtesy of the curator of the collection of Hymenoptera of the Berlin Zoological Museum, Prof. H. Bischoff, to reexamine Pallas's specimen, as well as his unpublished manuscript. Pallas gives in his manuscript the following indication about the origin of this Caucasian yellow bee: "Ad Caucasum lecta, itemque ex Hyrcania transmissa fuit." This means that Pallas obtained this bee near Caucasus and from the Southern coast of the Caspian Sea. It is evident that the Caucasian mountains were not the home of his species. Further on he writes: "Abdomen nudum, sessile, brevitur ovatum, testaceum basi, segmentis posteris nigro

marginatis vel totis piceis, cano subfimbriatus, presertim subtus." It is clear that this description concerns a yellow bee. The small size and pronounced yellow coloration of the specimens preserved in the Berlin Museum permit us to conclude that the form described by Pallas and Gerstäcker under the name *Apis remipes* is certainly not the gray mountain bee.

We have already shown in an earlier part of this paper that the Italian bees are quite independent of the yellow Caucasian bees. This allows us to consider the yellow Caucasian bees as a form independent of *Apis mellifera ligustica* Spinola. Diagram *D* on figure 20 shows the scheme of relationship between *Apis mellifera mellifera*, *Apis mellifera caucasica*, and *Apis mellifera remipes*. There is a general trend of change from the north of Russia to Transcaucasia (Migri). *Apis mellifera mellifera* indicates the northern type of bees: *Apis mellifera remipes* is the expression of the southern type. But this trend is broken by the mountain chain populated by *Apis mellifera caucasica*, which is in most of its characteristics a reversion towards the northern type (except for the tongue length and the relative length of legs). The difference in tongue length between the Italian bees and the Caucasians gives certain indications that the rate of change in north-south direction in the East is more rapid than in the West. A very slight hint supporting this hypothesis is given by the fact that in Eastern parts of European Russia, on the same parallel of latitude, the bees seem to have a longer tongue than in localities situated farther west. It is very likely that the lines of identical racial characteristics of bees have the same south-western, north-eastern slope as do the summer months isotherms in Eastern Europe.

GEOGRAPHICAL VARIATION OF THE HONEY BEE IN RELATION TO THAT OF OTHER ANIMALS AND SOME PROBABLE EXPLANATIONS OF ITS SIGNIFICANCE

The purpose of the present section is to connect our findings on the variation of the honey bee with data derived from the study of other animals. As is clear from the previous discussion of the variation of different races of the honey bee, we consider this as one of the cases of geographical variation of a species along the area of its distribution. Looking around for material suitable for comparison we have to confess that such data are not very abundant. Although the insects have always been favorite objects for the discussion of the problem of variation we do not have any extensive work on the biometry of insects. Entomological magazines are full of descriptions of varieties, usually without any consideration of the importance of the biometrical method. It seems, therefore, that at the present moment variation of the honey bee is better known in a quantitative sense than that of any other insect.

Turning our attention to other groups of animals we do not find the situation to be consolatory, although examples of geographical variation are known to every taxonomist working in this or that particular group of animals. Series of analogous examples are brought together in some of the modern books like those of Hesse (31), Berg (19), and Robson (68), but unfortunately most of them do not have an exact quantitative treatment. Only a few groups of animals have been studied on the basis of exact measurements and statistical discussions of the numerical data. Looking for examples of such work we may refer to the investigations of Heincke (30) and J. Schmidt (71, 72) on fishes, Sumner (74, 75) on *Peromyscus*

BOSTON UNIVERSITY
COLLEGE OF LIBERAL ARTS
LIBRARY

(Rodentia) and Crampton (23) on Mollusca. The brilliant investigations of Schmidt and Sumner are particularly interesting, because of the application of experimental methods in the evaluation of the stability of subspecific (racial) characteristics. Our findings confirm perfectly the statements of these authors. Schmidt writes (71) "It is pointed out that the term 'races' of fish, as characterized by our population analysis, is only a statistical expression. The 'Race' is a mixture of different genotypes, where the proportions between these primarily, the environment only secondarily, exert determinative effects upon the average values which characterize the race." This is in accord with the phenomenon which we described above under the name of family variation.

As far as our experience goes the racial characteristics are strictly inherent. For instance, Schmidt says (72) that "the results of our transplantation experiments with *Zoarces* agree with the experiment with *Lebistes* previously described and confirm that the difference, proved to exist between the two populations, is of hereditary (genotypical) nature." All our experience with transportation of southern races of bees to northern localities in Europe and to the United States of America show the inheritance of racial characteristics. In that respect our data are in perfect agreement with Schmidt's (72) and Sumner's (75) findings on the stability of the subspecific (in other words racial) characters under changed conditions of the environment.

In regard to the origin of the differences of geographical forms, the general tendency of the investigators who have studied this phenomenon from the biometrical and experimental points of view is not to lay much stress on the influence of external conditions on the manifestations of geographical variation. Much more importance is attributed to the internal, i.e., hereditary factors. Crampton writes (23, p. 311) "In a word, the rôle of the environment is to set the limits to the habitable areas or to bring about the elimination of individuals whose qualities are otherwise determined—that is, by congenital factors," Schmidt (72, p. 10) concludes that

> the investigations and experiments with *Zoarces* described above have rendered new evidence of the correctness of the view, that the race characters in fishes are of a hereditary nature, i.e., that they are first and foremost determined by internal factors. That they are however on the other hand to a certain extent influenced by external factors, is here for the first time experimentally proved for one of our northern species of fishes. . . . . In view of the investigations hitherto undertaken the gradation of the average number of vertebrae has to be interpreted not as a direct effect of external conditions (the salinity or other factors acting parallel to it) but as a result of a selection.

Sumner (75, p. 254), discussing the problem of the origin of specific characters, expresses a very disappointing opinion "that we are not yet prepared to frame any adequate general hypothesis as to species formation."

H. F. Osborn in a recent paper (61) summarized in a brilliant form all of our knowledge relating to the problem of species splitting. He distinguishes distinctly the conception of mutation and speciation. The mutations arise suddenly. The process of speciation, on the other hand, indicates a phenomenon of differentiation of a species into subspecies connected with intergrading forms. Our material on bees must be listed in the category of phenomena of speciation. So far as the causes of this process are concerned Osborn leaves the reader without explanations.

The opinions of the leading authorities in this particular problem which have been quoted give evidence of the fact that

at the present time we do not have any adequate explanation of the origin of geographical variation. A simple Lamarckian explanation, very popular among paleontologists and taxonomists, cannot be taken into serious consideration because of the lack of any credible experimental evidence of the inheritance of acquired characters.

We think it worth while, in looking for the explanation of the origin of geographical races, to turn our attention to the biological significance of the characters studied. In starting our work on the biometry of the honey bee—an insect of economic importance—we naturally did not fail to include in the investigation characters which have direct biological importance for the animal itself and hence for the beekeeper. Such characters are: the length of the tongue, size of the hind legs, size of the surface of the wax gland, and the size and number of hooks of the wings. It is very probable that all our biologically significant characteristics have a definite relation to the conditions of existence. The longer tongue of southern bees is probably connected with peculiarities of nectar secretion in the south as compared with the more northern localities. Michailov (39) suggested that the longer tongue of southern bees is an adaptation to dry conditions which lead to a lower level of nectar in the south, and thus compel the bee to have a longer working organ. We expressed (3) the hypothesis that the southern bees are obliged to have a longer tongue, not only because of a lower nectar level, but also because of a probable difference in the composition of the whole nectar secreting flora. It has been reported by many beekeepers that the southern, and particularly the Caucasian, bees can fly longer distances gathering nectar, and it is probable that their wings are in consequence more developed and have a larger number of hooks. The smaller size of the wax glands is probably connected with the condition that the bees in the South have perhaps less need to work upon the reinforcement of their nest. Hence the differences in the tongues, the wings and the wax glands (also probably in the first joint of the tarsus of the last pair of legs) may be considered as adaptations to different biological ends. It is probable that these characters have been developed by means of natural selection. Other characteristics like the general size of the body and coloration cannot at the present moment be even hypothetically evaluated as having any biological importance for the organism.

This discussion must stop here, unfortunately, because of the absence of comparable material on other insects. Aside from some indications as to the higher coloration and smaller body dimensions of southern insects we know little or nothing about this subject. It would be very desirable to develop active work in this direction. The large zoological museums furnish a tremendous number of opportunities for such investigations. It would be of great benefit to establish in large museums especially equipped biometrical laboratories, devoting their attention to geographical variation. The museums are real treasuries of material which, as a rule, has been worked upon only from routine taxonomical and zoogeographical points of view.

SUMMARY

1. This paper represents the results of five years of study on the biometry of the most important European races of the honey bee (*Apis mellifera* L.) being based on materials collected in their native locations as well as materials from the United States where the honey bee was

imported from Europe. The conclusions of this paper are based on the following material: (1) original measurements of more than 3000 specimens from 47 localities, (2) measurements of 10,000 specimens done in Russian Apicultural Experimental Stations and published mostly in previous papers by the author, (3) material (about 1500 specimens) published by A. S. Michailov and reproduced here in partly recalculated form.

2. One of the indispensable requirements in racial investigations on social insects is the consideration of differences which exist between colonies. The existence of family or colony variation is in this particular case demonstrated by the variation of number of hooks of bees belonging to different colonies. The variation of a colony represents only a certain part of the variation of the race. Hence it is advisable to take for racial investigation specimens from as many colonies as possible.

3. A. S. Michailov's data show that the following conditions of development have a pronounced effect on the body size of the worker bees: (1) the season of the development, (2) the temperature of the surroundings during the pupal stage, (3) the size of the cell, (4) feeding by nurse bees of different age, and (5) individuality of the colony. Recalculations of some data published by W. P. Michailov permit the addition to this list of the strength of the colony as a factor connected with the tongue length of the members of the colony.

Our original observations show that the size of the body is correlated with the reduction of the larval feeding period. In many cases the changes in absolute dimensions of the bee body have been accompanied by changes in proportions of the body. It is difficult to draw general conclusions concerning the character of the changes in proportions under the influence of different factors, each of them having a rather specific effect.

4. The geographical variation of bees is shown in the clearest form in the distribution of the average tongue length on the plain of European Russia. Bees even from neighboring localities differ in the average length of tongue, by showing a definite increase in length to the south. A linear equation is given connecting the latitude of the locality and the average tongue length.

5. Comparing bees from a northern locality (Middle Russia) with bees from the south (South Russia, North Caucasus and Italy) it can be seen that the southern bees are characterized by the smaller size of the body, larger number of hooks (North Caucasian bees being an exception), smaller relative surface of the first wax gland, relatively broader wings, and relatively longer legs. Our limited material on drones permits us to draw a conclusion about the smaller size of the drones in southern localities.

6. The black and yellow races of bees cultivated in the United States keep the same peculiarities which characterize the southern (yellow) and northern (black) races in Europe. They do not show any geographical variation analogous to that of Eastern Europe. On the other hand in regard to the variation of the tongue length the Americanized Italian yellow bee is not homogeneous, different apiaries being characterized by their own average tongue length. Being larger than Italian bees from queens born in Italy, American Italians are very close to the Ukrainian bees, differing from them, of course, in the coloration of the body and partially in the tongue length.

7. The bees inhabiting North Caucasus and Transcaucasia (Migri bees) represent a further step in the north-south scheme of

the variation in the honey bee. The mountain gray Caucasian bee is a reversion to the northern type, differing in many characteristics from the yellow Caucasian bees living in valleys.

A high relative length of the legs must be considered as a peculiarity of all Caucasian bees.

In respect to the length of the tongue the Caucasian bees have the longest tongue among all races studied up to the present moment.

8. The transportation of bee races to new countries gives good material for judging the stability of racial characteristics. In that respect the bee races cultivated in the United States bring evidence that the racial differences between black and yellow races remain unchanged even in new habitats. Artificial selection (or perhaps the admixture of Cyprian blood) is the cause of the fact that the Italian bees cultivated in the United States are even lighter colored than the Italians from Italy. The size of the body of the American Italian bees seems to be larger than that of native Italian bees. There are evidences that the tongue length of bees inhabiting different parts of European Russia is also an inherent characteristic.

9. Parallel to the geographical variation in physical characteristics runs the variation of biology and behavior. Swarm instinct, number of extra queens, number of queen cells, preference in collecting the nectar from different plants, gentleness and capping of the combs are different in different races.

10. The geographical variation of the honey bee (*Apis mellifera*) has to be considered as one example of the geographical variation of animals in general. Two laws of geographical variation in the honey bee can be listed as follows: (1) the variation is continuous and gradual, and (2) the characters of geographical forms may be correlated (positively and negatively) or may vary independently from each other. In cases of gradual geographical variation it is proposed to use special names to designate the extreme links in the chain of geographical forms. Four new names are accepted to specify the geographical races of bees: *Apis mellifera mellifera* L. naming the North European black type of bees; *Apis mellifera ligustica* Spinola, the southwestern type of bees (Italian bees); *Apis mellifera remipes* Gerstäcker, south eastern type of Caucasian bees; and *Apis mellifera caucasica* Gorbatschev, the gray mountain Caucasian bee.

11. The geographical variation of the honey bee as compared with data on the geographical variation of other animals does not allow us at the present moment to draw any definite conclusions concerning its origin. Taking into consideration Osborn's distinction between mutation and speciation we have to list our material on the honey bee in the category of phenomena of speciation.

Some of the characteristics can be discussed from the point of view of their biological significance. Such characteristics are: the length of the tongue, size of the hind legs, size of the surface of the wax gland and the size of the wings and the number of hooks on them. It is probable that these characteristics have been developed by means of natural selection. Other characteristics like the general size of the body and coloration cannot at the present moment be considered even hypothetically as having any biological importance for the organism.

12. It is suggested, for the promotion of quantitative investigations in the field of geographical variation, to establish specially equipped biometrical laboratories in large zoological museums.

LIST OF LITERATURE

(1) Alpatov, W. W. 1923. Die Decapoden des Weissen, Barents und Karameeres. (In Russian, with a German summary.) Berichte des Wissenschaftlichen Meeresinstituts, Lief. 7, pp. 1–36.

(2) ———. 1924. Die Definition der untersten systematischen Kategorien vom Standpunkte des Studiums der Variabilität der Ameisen und der Crustaceen. Zool. Anz., Bd. 60, pp. 161–168.

(3) ———. 1925. Über die Verkleinerung der Rüssellänge der Honigbiene vom Süden nach Norden hin. Zool. Anz., Bd. 65, pp. 103–111.

(4) Alpatov, W. W., and Tjunin, F. A. 1925. Beiträge zur Kenntnis der Variabilität der Rüssellänge bei der Honigbiene. (In German, with a Russian summary.) Rev. Zool. Russe, Vol. 5, pp. 79–108.

(5) Alpatov, W. W. 1926. Der Rüssel der Kasaner Arbeitsbiene in variations-statistischer Bearbeitung. (In Russian with German summary.) Bull. of Kasan Agr. Exp. Sta., No. 4, pp. 23–33.

(6) ———. 1927. The cardinal problems in the study of the Caucasian bee races. (In Russian.) Ptschelowodni Mir, Vol. 1, pp. 3–8.

(7) ———. 1927. On the variability of the hooks on the hind wings of the honey bee. (In Russian.) Ptschelowodnoje Djelo. January, 1927, pp. 1–7.

(8) ———. 1927. On the amelioration of the bee races. Ptschelowodnoje Djelo. No. 89, pp. 372–377. (In Russian.) The same in English, Bee World, March, 1928.

(9) ———. 1927. Biometrical study on bees of Middle and Southern Russia. (In Russian, with English summary.) Rev. Zool. Russ., Vol. 7, livr. 4, pp. 31–74.

(10) ———. 1928. On the tongue length of bee races cultivated in the United States of America. (In Russian.) Ptschelowodnoje Djelo, October, pp. 449–453.

(11) ———. 1928. Variation of hooks on the hind wing of the honey bee (Apis mellifera L.) Biol. Bull., v. 60, No. 3, pp. 209–234.

(12) ———. 1928. On the variability of the tongue length of the Caucasian gray bees and its inheritance. (In Russian with an English summary.) Ptschelowondi Mir, No. 1–3, pp. 4–11.

(13) ———. 1928. On the improvement of the bee races. Reports of the Maryland State Beekeepers Association, Vol. XII, p. 361–372.

(14) Alpatov, W. W. 1928. The influence of the conditions of development on the organism of the worker bee and the queen. American Bee Journal, V. 68, No. 3, pp. 115–117.

(15) ———. Variability in the honey bee tongue biometrically investigated and practical questions connected with the problem of the selection of the honey bee. (In Press, Proceedings of the IV International Entomological Congress.)

(16) Armbruster, L. 1923. Wie untersucht man Bienenstämme und Bienenkreuzungen auf ihre Farbe? Archiv für Bienenkunde, V. 5, No. 4.

(17) Arnoldi, K. 1926. Studien über die Variabilität der Ameisen. Z. f. Morphologie und Ökologie der Tiere, V. 7, pp. 254–278.

(18) Becker, F. 1925. Bienenkönigin und Arbeiterin als phänotypische Erscheinungsformen. Erlanger Jahrbuch für Bienenkunde, Bd. 3.

(19) Bero, L. S. 1926. Nomogenesis or Evolution Determined by Law. London, pp. xviii + 477.

(20) Buttel-Reepen, H. von. 1906. Apistica. Beiträge zur Systematik, Biologie, sowie zur geschichtlichen und geographischen Verbreitung der Honigbiene (Apis mellifera L.), ihrer Variatäten und der übrigen Apisarten. Mitt. Zool. Mus. Berlin, V. 3, pp. 17–201, illust.

(21) Briuchanenko, A. N. 1926. Beekeeping. Moscow, 2d edition, pp. 562.

(22) Chochlov, B. P. 1916. Investigations on the length of the bee tongue. Ministry of Agriculture, Petrograd. p. 17–41 with 8 plates. (In Russian.)

(23) Crampton, W. E. 1916. Studies on the variation, distribution and evolution of the genus Partula. Carnegie Institution of Washington Publ. No. 228, pp. 1–311.

(24) Dementiewa, T. 1927. Materialien zur Kenntniss der Variabilität der niederen Crustaceen. Arbeiten der Biologischen Station zu Kossino. Lief. 5, pp. 18–30.

(25) Dzierzon, John. 1861. Rationelle Bienenzucht (English translation). 1882, pp. 350.

(26) Gorbatschev, A. N. 1916. The gray mountain Caucasian bee (Apis mellifera Caucasica) and its place among other bees. Tiflis. (In Russian with English summary.)

(27) Götze, G. 1926. Zur Züchtungsbiologie, Variabilitätsstudien an der Honigbiene. Preussische Bienenzeitung in Mohrungen, No. 9, 1–8.

(28) Gubin, A. F. The Department of Apiculture of the Moscow District Agricultural Experiment Station and its work on the rôle of the honey bee in pollination of agricultural plants. (In Press, Proceedings of the 4th International Entomological Congress.)

(29) ———. 1918. Red clover and Caucasian bees. Opitnaja Paseca, May-June, pp. 257–263. (In Russian.)

(30) Heincke, F. 1898. Die Naturgeschichte des Herings. Abhandlungen des Deutschen Seefischerei Vereins, Berlin, P. I, pp. cxxxvi + 138, P. II, pp. xi + 223.

(31) Hesse, R. 1924. Tiergeographie auf ökologischer Grundlage. Jena.

(32) Klingen, J. N. 1913. On the practical importance of red clover fertilization by Caucasian bees. Proceedings of the Society of the Orel District. (In Russian.)

(33) Koshevnikov, G. A. 1900–1905. Materials to the natural history of the honey bee. Vol. I and II. Moscow, Soc. des Amateurs des Sciences Naturalles.

(34) ———. 1925. The variability of queens and the problem of race improvement in apiculture. Ptchelowodnoje Djelo. Moscow. (In Russian.)

(35) Kulagin, N. M. 1906. Die Länge des Bienenrüssels. Zool. Anz. Bd. 29.

(36) Kurotchkin, A. J. 1918. The tongue of the Nizhni Nowgorod bees worked out biometrically. Opytnaja Paseca, No. 5–6, pp. 226–235.

(37) Loginov, W. J. 1926. Über die Anwendung Biometrie in der Bienenzucht. Bull. of Kasan Agr. Exp. Station No. 4, pp. 3–22. (In Russian with a German summary.)

(38) Martynov, W. A. 1901. A bee colony exclusively with drone combs. (In Russian.) Proceedings of the Moscow Agricultural Academy, v. 7, No. 1.

(39) Michailov, A. S. 1914. On the tongue length of the bees from Tcherepovetz District in connection with the problem of the local differences in tongue length. Ptschelowodnoje Djelo. February. (In Russian.)

(40) ———. 1916. On the probable increase of the bee body size in the northern direction. (In Russian.) Opytnaja paseca, No. 11, pp. 9–10.

(41) ———. 1916. On the increasing variability of the honey bee from north to south. (In Russian.) Opytnaja Paseca, No. 12, pp. 13–14.

(42) Michailov, A. S. 1916. Ueber eine lineare Korrelation zwischen der Rüssellänge der Honigbiene und der geographischen Breite im ebenen europäischen Russland. Archiv für Bienenkunde, V. VII, No. 1, pp. 28–33.

(43) ———. 1927. Heincke's method as applied to the determination of the bee races. (In Russian.) Opytnaja Paseca, No. 3, pp. 74–77.

(44) ———. 1927. On the correlation between the length of the right front wing and the number of the hooks on the right hind wing of the Tula bee. (In Russian.) Opytnaja Paseca, No. 4, pp. 112–115.

(45) ———. 1927. The determination of the weight of the newly emerged bees as a method to measure their size. (In Russian.) Opytnaja Paseca, No. 5, pp. 145–148.

(46) ———. 1927. Der Einfluss einiger Lebenslagefaktoren auf der Variabilität der Honigbiene. Archiv für Bienenkunde, v. 8, No. 8, pp. 1–15.

(47) ———. 1927. The relation between the productivity of the bee colony and some measurable characters. (In Russian.) Opytnaja Paseca, No. 10, pp. 314–317.

(48) ———. 1927. Is there any correlation between the strength of the colony and the size of its bees? (In Russian.) Opytnaja Paseca, No. 11, pp. 337–340.

(49) ———. 1927. Do the dimensions of the bees change with their age? (In Russian.) Opytnaja Paseca, No. 12, pp. 370–373.

(50) ———. 1927. On the biometry of the gray Caucasian bee. (In Russian.) Ptschelowodni Mir, No. 3, pp. 84–86.

(51) ———. 1927. Über die Saison-variabilität der Honigbiene. Archiv für Bienenkunde, Vol. VIII, Heft 8, pp. 16–24.

(52) ———. 1927. Über den Zusammenhang zwischen dem Umfang des Bienenkörpers und seinen Teile. Arch. für Bienenkunde, VIII Jahrg., Heft 8, pp. 25–33.

(53) ———. 1928. Contribution to the problem of acclimatisation of gray mountain Caucasian bee races in the middle region of U. S. S. R. (In Russian.) Opytnaja Paseca, No. 1, pp. 11–15.

(54) ———. 1928. External characters of bees reared by old and young nurse bees. (In Russian.) Opytnaja Paseca, No. 3, pp. 110–112.

(55) Michailov, A. S. 1928. Effect of the colony upon the bees reared in it. (In Russian.) Opytnaja Paseca, No. 7, pp. 299–302.

(56) ———. 1928. Ueber die geographische Variabilität der Honigbiene (Apis mellifera L.) im ebenen europäischen U. S. S. R. (Russland). Zool. Anzeiger; V. 77, pp. 29–36.

(57) Michailov, B. P. 1926. The Permian bee. (In Russian.) Opytnaja Paseca, No. 7–8, pp. 9–11.

(58) Mosolevsky, G. 1928. Abkhasian bees. American Bee Journal, v. 58, No. 10, pp. 524–525.

(59) Newell, Wilmon. 1915. Inheritance in the honey bee. Science, N.S., V. 41, No. 1049, pp. 218–219.

(60) Nolan, W. J. 1928. Seasonal brood-rearing activity of the Cyprian honey bee. Journal of Economic Entomology, V. 21, No. 2, pp. 392–403.

(61) Osborn, H. F. 1917. The origin of species. V. Speciation and mutation. American Naturalist, Vol. 61, No. 672, pp. 5–42.

(62) Palenitschko, Z. 1927. Zur vergleichenden Variabilität der Arten und Kasten bei der Ameisen. Z. f. Morpholog. und Ökologie, V. 9, pp. 410–438.

(63) Pearl, R. 1909. The frequency constants of a variable, $z = f(x_1, x_2)$. Biometrika, Vol. VI, pp. 437–438.

(64) Pearson, K. 1897. On a form of spurious correlation which may arise when indices are used in the measurement of organs. Proc. Roy. Soc., Vol. 60, pp. 489–498.

(65) Phillips, E. F. 1918. Beekeeping. New York, (Macmillan Co.). Pp. xxvii + 490.

(66) Philiptschenko, Jur. 1918. La variabilité chez les abeilles et la statistique de variation. Journal russe de Zoologie, Vol. 3. (In Russian with a French summary.)

(67) Postojalko, A. B. 1902. Bee races and their practical value. Proceedings of the Caucasian silkworm culture station. (In Russian.) See also other articles of the same author in Ptschelovodni Mir, 1917–1918. (In Russian.)

(68) Robson, G. C. 1928. The Species Problem. Edinburgh and London. pp. vi + 283.

(69) Root, A. I. and E. R. 1923. The ABC and XYZ of Bee Culture. Medina, Ohio. Pp. 960.

(70) Rösch, G. A. 1925. Untersuchungen über die Arbeitsteilung im Bienenstaat. Ztschr. f. Verg. Physiologie, Pp. 571–631.

(71) Schmidt, J. 1917. Zoarces viviparus L. and the local races of the same. Comptes rendus des travaux du Laboratoire de Carlsberg, 13me vol., 3 livr.

(72) Schmidt, J. 1917–1923. Racial investigations. V. Experimental investigations with Zoarces viviparus L. Comptes Rendus des Travaux du Laboratoire Carlsberg, v. 14.

(73) Semenov-Tian-Shansky, A. P. 1910. Die taxonomischen Grenzen der Art und ihrer Unterabteilungen. Berlin (Verlag Friedländer und Sohn.)

(74) Sumner, F. B. 1918. Continuous and discontinuous variations and their inheritance in Peromyscus. Amer. Naturalist, v. 52, pp. 177–208.

(75) ———. 1923. Some facts relevant to the discussion of the origin and inheritance of specific characters. American Naturalist, v. 57, pp. 238–254. (See also numerous publications on Peromyscus mostly in American Naturalist and Journal of Mammology.)

(76) Thomson, E. Y., Bell, J., and Pearson, K. 1909. A second cooperative study of Vespa vulgaris. Biometrika, Vol. 7, 48–63.

(77) ———. 1911. A third cooperative study of Vespa vulgaris. Biometrika, Vol. 8, pp. 1–12.

(78) Warren, E. 1902. Variation and inheritance on the parthenogenetic generations of the Aphis Hyalopterus trichosus (Walker). Biometrika, Vol. 1, pp. 129–154.

(79) ———. 1908. Some statistical observations on termites. Biometrika, Vol. VI, pp. 329–347.

(80) Watson, Lloyd R. 1917. Controlled Mating of Queenbees. Hamilton, Illinois. Pp. 1–50.

(81) ———. 1928. Controlled mating in honey bees. The Quarterly Review of Biology, Vol. III, No. 3, pp. 376–390.

(82) Yule, G. Udny. 1919. An Introduction to the Theory of Statistics. 5th edition.

(83) Zander, E. 1923. Beiträge zur Variabilität und Vererbung bei der Honigbiene. pp. 1–65. Erlanger Jahrbuch für Bienenkunde, Bd. 1.

(84) ———. Handbuch der Bienenkunde in Einzeldarstellungen, Vol. I–V. Stuttgart.

EXPERIMENTAL STUDIES OF BIRD MALARIA

By ROBERT HEGNER

Department of Protozoology, The Johns Hopkins School of Hygiene and Public Health

INTRODUCTION

HUMAN malaria is undoubtedly the most important of all diseases in large areas of tropical and subtropical regions. It has been studied intensively by large numbers of first rate investigators during the past forty years, but there are still many problems to be solved, both scientific and applied. Some of these cannot be studied satisfactorily in man, although the recent discovery that general paralysis can be alleviated by malarial treatment has given an opportunity for controlled experiments with human beings from which results of importance have been derived. Fortunately birds are also infected with malarial parasites which resemble closely in their morphology and life-cycles the corresponding parasites of man. It is thus possible to use birds as experimental laboratory animals and to subject them to various conditions not possible in the case of human beings. Several very important discoveries in malaria have been made with the aid of birds. For example, MacCallum (1897) first observed in the blood of birds the process of gametogenesis and fertilization which had been troubling investigators for many years; Ross (1898) by his studies of bird malarial parasites proved that mosquitoes transmit malaria from one vertebrate host to another; and Roehl (1926) developed the valuable new therapeutic agent known as plasmochin as a result of experiments on birds.

During the past ten years, since the Johns Hopkins School of Hygiene and Public Health has been organized, canary birds infected with malarial parasites have been maintained in the laboratory of protozoology, and a number of investigators have carried out experimental studies with these organisms. In the following pages the writer has attempted to bring together some of the interesting results of these studies.

SPECIES OF BIRDS INFECTED IN NATURE

Malarial parasites belonging to the genus *Plasmodium* have been reported from many species of wild birds living in many countries; apparently they are especially common in birds of tropical and semi-tropical regions. According to Huff (1927) infections have been noted in at least 79 species of birds. These belong to at least 15 families included in the orders Anseres, Paludicolae, Columbae, Raptores, Pici, Passeres, and others. More species of the order Passeres have been found with infections than those of any other order, and members of the family Fringillidae appear to be particularly susceptible. The parasites now being used in the laboratories in the United States were obtained from English sparrows by Whitmore in New York in August 1913, by Hartman in Baltimore in October 1924,

and by Huff in Hampton, Virginia, in September 1926.

GENERA AND SPECIES OF MALARIAL PARASITES IN BIRDS

Danilewsky (1885) was the first to report pigmented parasites in the red blood corpuscles of birds. Five years later, Grassi and Feletti (1890) gave to this organism the name *Haemamoeba praecox*. The genus name *Proteosoma* was later applied to it by Labbé (1894) and is still often used. Careful investigations have demonstrated, however, that the malarial

FIG. 1. GAMETOCYTES OF (A.) PLASMODIUM PRAECOX; (B.) P. CATHEMERIUM; AND (C.) P. INCONSTANS, SHOWING DISTINGUISHING CHARACTERISTICS

The dark oval body is the nucleus of the red cell. (After Hartman, 1927b.)

parasites of man and birds belong to the same genus; hence the proper generic name of the latter is *Plasmodium*.

A genus of blood-inhabiting protozoa that is common in birds and resembles the genus *Plasmodium* in certain respects is *Haemoproteus* (*Halteridium*). A simple method of distinguishing one from the other is to observe the position of the nucleus of the infected red cell in relation to the parasite; in *Plasmodium* the nucleus is ordinarily pushed to one side by the invading organism; whereas in *Haemoproteus* the parasite grows around the nucleus without displacing it. Three kinds of malarial parasites in birds were reported by Celli and Sanfelice (1891) but were not described sufficiently to be recognizable. In practically all of the papers published up to the year 1927 the organisms studied were supposed to belong to a single species, usually called *Plasmodium praecox*. Hartman (1927b), however, believes that at least three species exist. For one of these, isolated from the Whitmore strain, he retains the name *P. praecox;* for the second, which is known as the Hartman strain, he proposes the name *P. cathemerium*, and for the third strain, obtained by Huff in Virginia, he proposes the name *P. inconstans*. Evidence has been secured by Manwell that the Whitmore strain may consist of two distinct varieties or species. The most important diagnostic characteristics of the three species as given by Hartman are as follows: *P. praecox* (fig. 1a) has elongated crescent-shaped gametocytes, schizonts that seldom occur in the peripheral blood, and an asexual cycle of about 24 hours (Hartman, 1927b); *P. cathemerium* (fig. 1b) has spherical gametocytes containing rather coarse, rod-shaped pigment granules, numerous schizonts in the peripheral blood, and an asexual cycle of 24 hours (Taliaferro, 1925; Hartman, 1927a); *P. inconstans* (fig. 1c) has nearly spherical gametocytes containing pigment granules that are approximately spherical and much smaller than those of *P. cathemerium*.

STAGES IN THE LIFE-CYCLE OF MALARIAL PARASITES

For the benefit of readers who are not familiar with the life-cycle of the malarial parasites the following brief account is presented (fig. 2). In nature the infective stage for the vertebrate host is a spindle-shaped body about 10 microns in length known as a sporozoite. Sporozoites are present in the salivary glands of infected mosquitoes and are injected into the

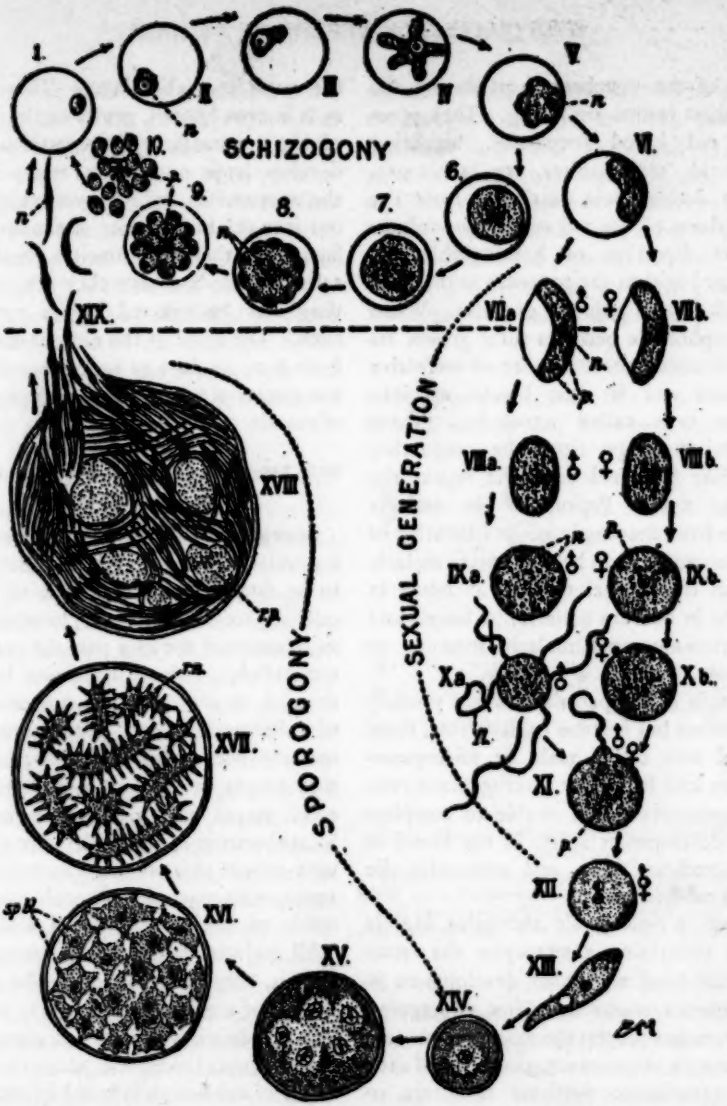


FIG. 2. DIAGRAM ILLUSTRATING THE LIFE-CYCLE OF PLASMODIUM FALCIPARUM IN MAN AND MOSQUITO

The stages shown above the line of dashes are passed through in the blood of man; those below the line, in the body of an anopheline mosquito. The asexual cycle (schizogony) begins with the sporozoite (XIX), which penetrates a red cell and becomes a trophozoite (I); this grows into a schizont (II–V), which segments into a number of merozoites (6–10), which in turn penetrate red cells and repeat the cycle. Some trophozoites develop into gametocytes (VI), which are of two kinds, microgametocytes (VIIa) and macrogametocytes (VIIb). The macrogametocyte breaks out of the red cell (VIIIb), becomes spherical (IXb), and throws off a polar body (Xb) thus becoming a mature macrogamete. The microgametocyte breaks out of the red cell (VIIIa), becomes spherical (IXa), and sends out 6 to 8 filamentous microgametes, one of which fuses with each macrogamete (XI), thus forming a zygote (XII). The zygote changes into an ookinete (XIII), which penetrates the stomach wall, where it rounds up into an oocyst (XIV). The oocyst grows large and within it arise hundreds of sporozoites (XV–XVII). These break out into the body cavity of the mosquito (XVIII–XIX) and some of them reach the salivary glands, where they are then ready to be inoculated into a new host. (From Hegner after Minchin.)

blood of the vertebrate host during the time these insects are biting. They penetrate red blood corpuscles, becoming amoeboid trophozoites, or schizonts, which derive their nutriment from the protoplasm of the red cell. By-products of the digestion of haemoglobin are deposited within the parasites in the form of dark brown pigment granules. When the trophozoite becomes fully grown its nucleus undergoes a number of successive divisions and it then breaks up into minute cells called merozoites. These merozoites escape from the corpuscles, penetrate fresh red cells and repeat the asexual cycle. Periodicity in malaria results from the simultaneous liberation of the merozoites. In benign tertian malaria of man the asexual cycle is 48 hours in length; in quartan malaria, 72 hours; and in estivo-autumnal malaria from 24 to 48 hours.

Certain of the parasites do not produce merozoites but become gametocytes; these are of two types, male or microgametocytes and female or macrogametocytes. The gametocytes are unable to complete their development while in the blood of the vertebrate host, and eventually die unless removed.

When a susceptible mosquito ingests blood containing gametocytes the latter are stimulated to further development in the insect's stomach. After undergoing a maturation process the macrogametocyte becomes a ripe macrogamete and the microgametocyte produces from six to eight whip-like processes which represent microgametes. Fertilization is accomplished by the fusion of one macrogamete with one microgamete, thus forming a zygote. The zygote elongates into a slug-like oökinete capable of locomotion. The stomach wall of the mosquito is penetrated by the oökinete, which becomes spherical and quiescent just beneath the outer epithelial layer. This oöcyst, as it is now known, grows at the expense of the surrounding tissue and within it develop large numbers of minute cells, the sporozoites, which eventually break out into the body cavity of the mosquito. Some of these sporozoites reach the salivary glands where they remain until they may be injected into a vertebrate host. The cycle in the mosquito requires from 8 to 20 days or more depending on the species of parasite and the temperature of the air.

THE RELATION OF THE PARASITE TO THE RED BLOOD CORPUSCLES

Laveran, who in 1880 first discovered the human malarial organism, believed it to be attached to the outside of the red cell. Most malarialogists, however, have since accepted the idea that the parasite is intracellular. Much discussion has been devoted to this problem, and a number of observations and experiments have recently been published which indicate that except in the sporozoite and merozoite stages the malarial organism is located within the red cell. Among those who oppose this view are Lawson (1913–1919), who reached the conclusion as the result of studies of stained slides that "All malarial parasites are extracellular, that is, they are attached to the external surface of the infected corpuscle and each parasite destroys several red corpuscles." Sinton (1922) supports this view as a result of subjecting infected human blood to hypertonic and hypotonic solutions; and De Langen (1925) comes to a similar conclusion because washing infected human blood cells in Ringer's solution brought about a reduction in the number of parasites in proportion to the number of red cells and apparently dislodged some of the fully grown parasites from the surface of the corpuscles. What appears

to be the best method of determining the actual position of the parasites in relation to the red cells is that used by Ratcliffe (1927). Fresh blood from birds containing numerous specimens of *Plasmodium praecox*, and human blood infected with *P. vivax* was fixed in Bouin's fluid, sectioned 1.5μ or 2 μ thick and stained with Harris' haematoxylin. Material prepared in this way showed the parasites to be invariably inside of the wall of the red blood corpuscles and hence intracellular (fig. 3).

HOST-PARASITE RELATIONS IN BIRD MALARIA

The subject matter involved in the study of bird malaria may be indicated in terms of host-parasite relations. The writer has recently given an account of the biology of host-parasite relations of human protozoa in general (Hegner, 1926) and of intestinal protozoa in particular (Hegner, 1927). The relations between host and parasite include the following subjects: (1) The epidemiology of transmission, which deals with the infective stage of the parasite and its method of reaching and invading the host; (2) The distribution of the parasite within the host and the factors that lead to its localization in certain organs or tissues; (3) The natural or passive resistance of the host, by which is meant the obstacles that must be met by the parasite at the time of an invasion; (4) The natural or passive resistance of the parasite, which enables it to overcome these obstacles; (5) The character of the parasite's attack; (6) Changes in the host due to the parasitic invasion, such as symptoms, pathological lesions, and acquired resistance; (7) Changes in the parasite due to residence in the host, involving increases or decreases in resistance and aggressivity; (8) Host-parasite adjustments during an infection, which result in the carrier condition, latency and relapse; (9) Biological and chemical therapy; (10) Methods by which the progeny of the invading parasites reach the outside of the body; (11) Host-parasite specificity, including host susceptibility and parasite infectivity; (12) Methods of prevention and control, which may be considered personal hygiene in the case of the individual and public health measures when communities are involved.

MATERIAL AND METHODS OF RESEARCH

As already noted the laboratory strains of bird malaria that have been studied in

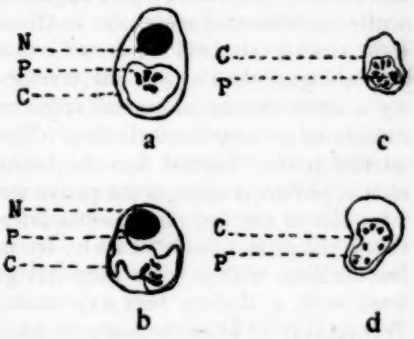


FIG. 3. MALARIAL PARASITES INSIDE OF RED BLOOD CORPUSCLES

Camera lucida drawings of sections of parasitized cells. *a, b, Plasmodium praecox* in red cells of bird. *c, d, P. vivax* in red cells of man. *C* = cell wall. *N* = nucleus of red cell. *P* = parasite. (After Ratcliffe.)

this country have come from English sparrows captured in New York, Baltimore and Virginia. These strains all grow and reproduce when inoculated into canary birds. Female canaries have been employed almost exclusively as experimental animals because of the much higher cost of male birds. As Whitmore (1918) demonstrated, the blood of a bird once infected remains infective for a long time, in many cases probably as long as the bird lives. Whitmore found one bird to be infective 29 months after it was inoculated, and Mazza (1924) obtained

infections with the blood of a bird 4 years and 2 months after the original infection. During most of these periods parasites are so few in number in the peripheral blood that they cannot be found in films made according to the usual methods. Thick films of the blood of birds are of no value in the study of malaria since the red blood corpuscles of birds are nucleated and when clumped together obscure any parasites that might be present.

To transfer infection to a fresh bird the vein on the inner side of the leg of an infected bird is punctured with a Hagedorn needle just below the ankle joint and from 50 to 100 mg. of blood are drawn into a Luer syringe of the $\frac{1}{4}$ or $\frac{1}{2}$ cc. size, containing a small amount of normal saline or citrated saline to prevent clotting. This mixture is then injected into the breast muscle, peritoneal cavity or the vein on the inner side of the leg. Intravenous injection is the most difficult method. It can best be done with a $\frac{1}{4}$ cc. Luer syringe fitted with a slightly bent #27 needle. The quantity of blood necessary to bring about an infection depends in part on the number of parasites in the infective blood and the natural resistance of the bird, but 100 mgs. of blood are practically always sufficient, unless the infective blood is obtained from a latent case, in which event 200 mgs. are often required.

Certain phases of the work require that gametocytes be distinguished from schizonts. The criteria for doing this, as worked out by L. G. Taliaferro (1925), are similar to those that have long been used in human malaria. The fully grown schizonts and gametocytes are about the same size and shape. The schizonts have mottled, medium-blue staining cytoplasm and pigment granules more or less clumped together. The macrogametocytes are characterized by darker-blue staining cytoplasm and dispersed pigment granules. In the microgametocytes the cytoplasm stains a very light blue and the nuclear material is often stellate in form.

A numerical expression of the degree of infection may be obtained in several ways. Ben-Harel (1923) obtained a ratio of parasites to corpuscles and the number of corpuscles present at a given time and from these data computed the number of parasites per cubic millimeter of blood. Frequent extraction of blood from a canary, which contains only about one cubic centimeter, interferes with the course of an infection; hence this method of counting has been discarded in favor of the following. A blood film is prepared and the ratio between the numbers of parasites and red cells is obtained by counting a number of microscopic fields. The proportion of parasites per 10,000 red cells is then calculated. If significant results are to be obtained one must know how large a sample must be examined, since this must be larger when a small number of parasites are present if a corresponding probable error is desired. A formula was worked out by Hartman (1927a) to determine how many corpuscles must be counted so that the probable error will be about 10 per cent of the observed number of parasites.

The desired probable error in equation form is: $PE_p = 1/10p$ in which PE_p is the probable error of the observed value and p is the observed value, i.e., the number of parasites per 10,000 red cells. The equation for the probable error is $PE = 0.67449\ \sigma$, in which σ is the standard deviation of the probability; and that for σ is $\sigma = \sqrt{\frac{p(1-p)}{N}}$, in which N is the number of units in the sample taken and p the observed frequency of the phenomenon under consideration. Substituting in the first equation above and solving for N we get $N = 45.494\frac{1-p}{p}$. This formula gives a means of calculating the size of sample (N number of corpuscles) which must be taken in order that the probable error of the relative frequency be one tenth of that frequency.

This formula is of value only if parasites are evenly distributed in a given sample. Tests indicate that the distribution of parasites in blood obtained as described above is uniform.

The periodicity of the asexual cycle in bird malaria necessitated a method of measuring the size of the schizonts. This was done by Taliaferro (1925) as follows. Parasites, 100 or 50 in number according to whether many or few were present, were drawn with a camera lucida, thus giving outlines of the organisms magnified 3000 diameters. The average length and breadth of these drawings were then obtained in micra, and their product divided by the number of parasites drawn. A modification of this method was used by Hartman (1927) who made camera lucida drawings and then computed their area in square microns with the aid of a planimeter.

Another method that was required to determine certain questions was that of obtaining the coefficient of variation. This was done by Taliaferro (1925) as follows:

1. The standard deviation was calculated by means of the formula.

$$\sqrt{\frac{\Sigma x^2}{n} - M^2},$$

in which x represents the magnitudes of the measurements (not their deviations), n the number of individuals and M the mean.

2. Finally, the coefficient of variation was derived by the formula.

$$\text{C.V.} = \frac{100\sigma}{M},$$

in which σ represents the standard deviation and M the mean.

DISTRIBUTION OF PARASITES WITHIN THE BIRD

Malarial parasites, when injected into a vertebrate host either in the sporozoite stage by mosquitoes or in the trophozoite stage by blood inoculation, are no doubt carried to all parts of the body in the blood stream. Malaria is often considered to be a disease of the peripheral blood, but the internal organs, especially the spleen, bone marrow, and liver, are liberally supplied with parasites. It has been suggested that the sudden decrease in numbers of parasites that occurs during the course of a normal infection might be the result of their segregation in certain tissues or organs. Ben-Harel (1923), Hartman (1927a), Dr. C. F. Scudder and Dr. R. F. Feemster (unpublished work) have all studied the tissues of the internal organs of birds at various stages of infections but have not found any evidence that migration from the blood into the tissues takes place. It seems certain therefore that the optimum habitat of bird malarial parasites is the blood stream and that the organisms are rather uniformly distributed throughout the body by the circulation of the blood.

An attempt was made by Boyd (1925) to determine the distribution of the parasites within the blood. He inoculated 10 birds with whole infected blood, 10 with washed red cells from infected blood and 10 with serum obtained by centrifuging whole infected blood and removing the serum with a pipette. No differences were found between the prepatent period and period of rise when whole blood and washed red cells were inoculated, but the prepatent period was over twice as long and only 4 of the 10 birds became infected when the serum was inoculated. This indicates that almost all of the parasites are within the red cells and very few in the serum.

PARASITOLOGICAL PERIODS

The parasitological periods differ for the three species of bird malarial parasites and

vary in length in different canaries. Data derived by Boyd (1925) from 30 birds infected with the Whitmore strain give a prepatent period of from 1 to 11 days with an average of 5.33 days, a period of rise of from 2 to 10 days with an average of 5.33 days, and a period of fall of from 2 to 12 days with an average of 5 days. Parasite curves showing low, intermediate and high infections with this strain are presented in figure 4 (MacDougall, 1927). A number of factors other than the natural resistance of the bird may be responsible for modifications in the parasitological periods. Huff (1927), who had an opportunity to study the course of infections with the three species of parasites named by Hartman (1927b), records the prepatent periods as follows:

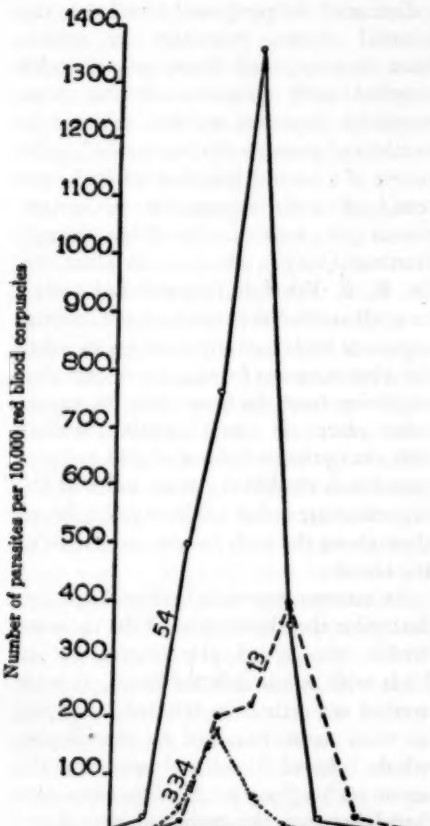


FIG. 4. CURVES REPRESENTING HIGH, INTERMEDIATE AND LOW INFECTIONS WITH BIRD MALARIA IN UNTREATED BIRDS

The data were obtained from birds 13, 54, and 334. (After MacDougall.)

PARASITE	NUMBER OF BIRDS	AVERAGE PREPATENT PERIOD
Plasmodium cathemerium	39	5.78 ±0.14
Plasmodium praecox	18	11.44 ±0.45
Plasmodium inconstans	10	8.5 ±0.37

The average lengths of the prepatent period as here given indicate that this characteristic may be of taxonomic value.

The effects of variations in the number of parasites inoculated upon the length of the parasitological periods were tested by Boyd (1925). Five birds that were inoculated with 100 parasites each did not become infected; that they were susceptible was proved by the fact that they were all infected later with larger doses. It seems probable that many of the parasites that are injected into the breast muscle of a bird are destroyed by phagocytes or other agencies and that the 100 parasites used met this fate. Of 7 birds inoculated with 1000 parasites each, 2 became infected and 5 did not. Five of 6 birds inoculated with 10,000 parasites each were positive. The effects of the number of parasites inoculated upon the length of the prepatent period is indicated in the following table, the coefficient of correlation being -0.522 ± 0.053.

NUMBER OF PARASITES USED FOR INOCULATIONS	LENGTH OF THE PREPATENT PERIOD IN DAYS												
	1	2	3	4	5	6	7	8	9	10	11	12	
1,000									1		1		2
10,000						1		1	1	1		1	5
100,000				1		1	2		3				7
200,000			2	1	8	1	2	2	1		1		18
1,000,000		2	4	3	6								15
5,000,000	1	4	4	3	2								14
10,000,000	4	3	4	3	3	1							18
20,000,000	1	2			1								4
	6	11	14	11	20	4	4	3	6	1	2	1	83

This table presents the prepatent period of 83 birds and proves conclusively that in general the length of this period depends directly upon the number of parasites inoculated, and that the greater the number of parasites the shorter the prepatent period becomes.

CLINICAL PERIODS

Symptoms of malaria, being largely subjective, have not been well determined for birds. Furthermore the temperature of birds changes so rapidly that thermometric readings are of little value. According to Hartman (1927a) one or more parasites to 100 red cells must be present before symptoms appear, although, as is to be expected, some birds with mild infections exhibit more severe symptoms than others with heavy infections. Symptoms, as in human malaria, occur soon after sporulation begins and continue for a shorter or longer period depending on the severity of the infection. The birds show signs of chills and fever, are more quiet than usual, and sit on their perches with their feathers ruffled up and often with the head under a wing. Weakness and loss of appetite may appear after the peak of the infection is passed.

NUMERICAL RELATIONS OF SCHIZONTS AND GAMETOCYTES

It is the general impression that the malarial sporozoites inoculated into the vertebrate host are of one type and all develop into schizonts. Some of them may develop into gametocytes but these would be very few in number and since they have no method of reproducing others of their kind would not account for the large number present in infections later in the course of the disease. According to Manwell the gametocytes of *Plasmodium cathemerium* can be found about 2 or 3 days after schizonts appear in birds infected by blood inoculation, and those of *P. praecox* at the end of the prepatent period, which is about 10 days in length. It seems certain that gametocytes as well as schizonts must develop from merozoites, even if some of them arise also from sporozoites. How this is brought about is problematical, but what we know of the cytological phenomena in the sex cells of higher organisms suggests that changes occur in the chromosome complex of certain schizonts such that all the merozoites produced by them develop into gametocytes or else similar changes take place during the segmentation of some of the schizonts, resulting in the formation of both schizont-producing and gametocyte-producing merozoites. What stimulates these hypothetical changes can hardly be conjectured.

Taliaferro (1925) found that during the acute period of an infection with *P. cathemerium* about 3 per cent of the parasites were gametocytes, and that during relapses and sometimes during the subpatent period the percentage of gametocytes ranged from 2 to 50. Huff (1927) made more detailed studies of the produc-

tion of gametocytes during the course of infections with *P. cathemerium*. Figure 5 presents curves of an acute infection followed by a relapse induced by feeding sugar to the bird on the days indicated by asterisks. The prepatent period was in this case 9 days in length. During the succeeding 4 days the number of parasites per 10,000 red cells (heavy solid line) rose to a peak of 800 and then decreased until 4 days later. This was followed by a subpatent period of 3 days and by a relapse, which was more severe than usual. During the acute infection gametocytes were first noted on the tenth day, increased to 220 per 10,000 red cells during the succeeding 3 days (light solid line) and disappeared from the peripheral blood 2 days later. They reappeared at the beginning of the relapse on the twentieth day, increased to 260 per 10,000 red cells 3 days later and then decreased until they disappeared 5 days later. The percentage of gametocytes to the total number of parasites, as indicated by the broken line, increased continuously and rapidly during the acute infection from 4 per cent on the tenth day to 84 on the fifteenth day. The percentage of gametocytes remained comparatively low during the relapse (from 6 per cent to 13 per cent). Huff concludes that since symptoms appear at the time the peak of the infection is reached, at which time the percentage of gametocytes is nearing the maximum, and since mosquitoes have a better chance of biting a bird that is sick, therefore the increase in the number of gametocytes as indicated has a significant effect on the epidemiology of transmission, mosquitoes being more apt to become infected at just the time when the birds are most susceptible to their bites. He also concludes that since there is no periodicity in the production of gametocytes, day-biting and night-biting mosquitoes have an equal chance of transmitting the organisms provided both types of these insects are susceptible.

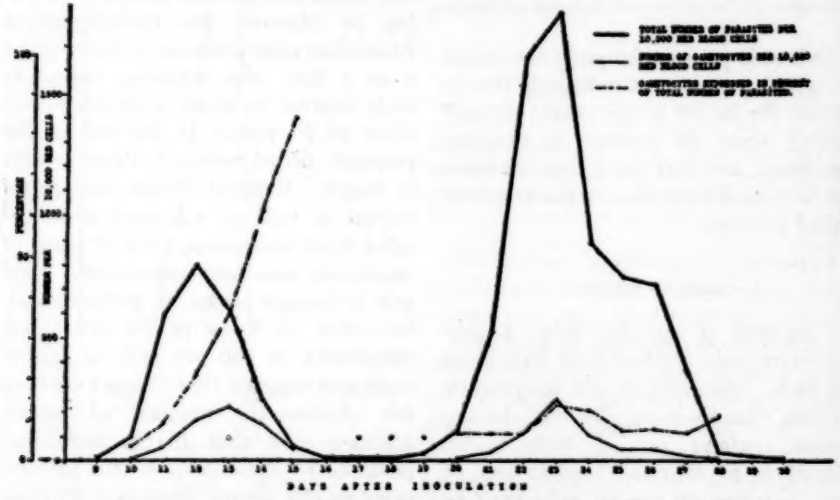


FIG. 5. COMPARATIVE NUMBERS OF GAMETOCYTES DURING AN ACUTE INFECTION OF BIRD MALARIA FOLLOWED BY A RELAPSE

The percentage of gametocytes (dots and dashes) increased throughout the acute infection but maintained almost a level during the relapse. Sugar was fed to this bird on the days indicated by asterisks. (After Huff.)

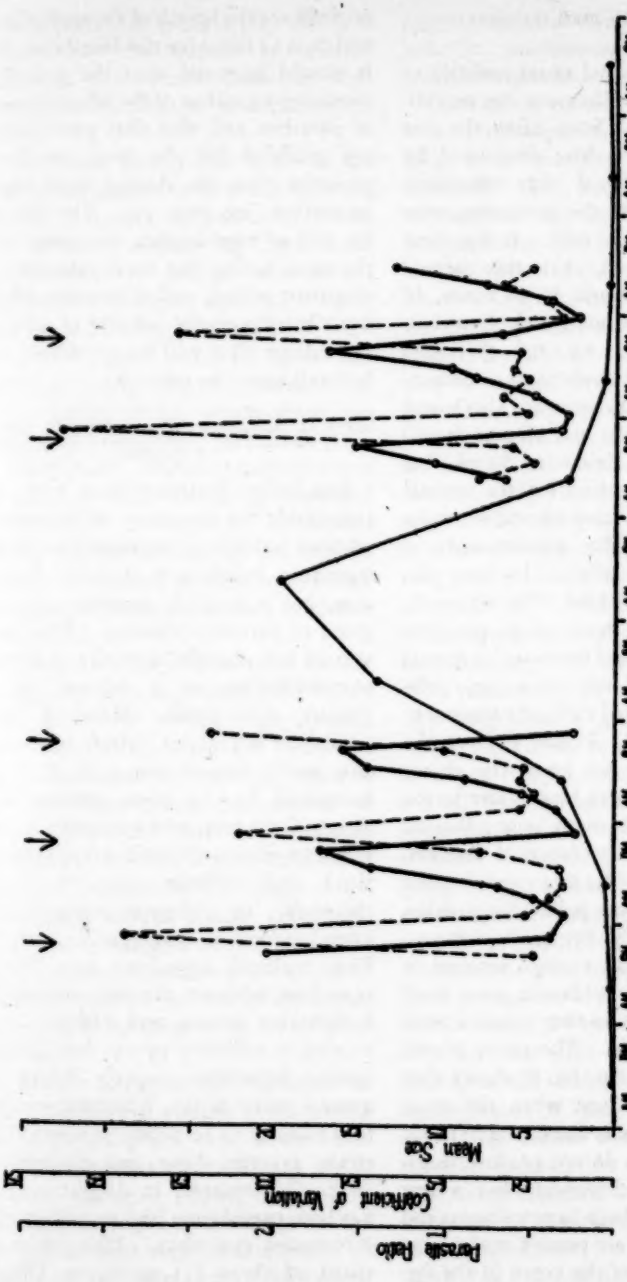


FIG. 6. MEAN SIZE (THICK LINE), COEFFICIENT OF VARIATION FOR SCHIZONTS (DASHES), AND NUMBER OF PARASITES PER 10 RED CELLS (THIN LINE) DURING AN INFECTION OF A BIRD WITH PLASMODIUM CATHEMERIUM

The distance between the peaks of the curve for mean size indicates the rate of reproduction, one generation per 24 hours; this rate of reproduction is not modified by the number of parasites destroyed. (After L. G. Tallisferro.)

PERIODICITY IN BIRD MALARIA

One of the principal characteristics of human malaria as a disease is the periodicity of symptoms. Soon after the true organism of malaria was discovered by Laveran it was found that symptoms appeared at the time the merozoites were liberated from the red cells. It was later definitely established that the asexual cycle of tertian malaria is 48 hours, of quartan malaria, 72 hours and of aestivo-autumnal malaria, 24 to 48 hours. Periodicity in bird malaria was demonstrated by Mrs. Taliaferro (1925) and confirmed by Drensky and Hegner (1926) and others. Mrs. Taliaferro found that there is a definite period for the asexual cycle in both the Whitmore and Hartman strains and that the synchronicity of reproduction is not affected by long passage from bird to bird.—For example, measurements were made of 50 parasites from one bird at 4 hour intervals for several successive days and the mean size, coefficient of variation, and ratio of parasites to red cells computed. Figure 6 gives the results. The curve for mean size shows that the parasites were largest late in the afternoon; there were many large schizonts at this time, some in process of division. Within a few hours the mean size dropped abruptly to its lowest point; the parasites observed were mostly very small schizonts. Then a more gradual average increase in size occurred as the schizonts grew until at the end of 24 hours they reached their maximum size again. The curve of the coefficient of variation (fig. 6) shows that variability was greatest when the mean size was lowest; this is due to the fact that all of the schizonts do not produce merozoites exactly synchronously but a few lag behind so that both large schizonts and small trophozoites are present at the same time. The peaks of the curve in the figure indicate the length of the asexual cycle, which is 24 hours for the Hartman strain. It should be noted that the periodicity continues regardless of the relative number of parasites and also that periodicity is not modified by the large number of parasites that die during each asexual generation (see page 75). The fact that the rate of reproduction was found to be the same during the acute infection, the subpatent period, and subsequent relapses has a bearing on the subjects of resistance and relapse that will be considered more in detail later (see page 77).

ASEXUAL REPRODUCTION WITHOUT LOSS OF VITALITY

Free-living protozoa have been used extensively for the study of the question whether unicellular organisms are able to reproduce indefinitely without fertilization, but very little attention has been given to parasitic protozoa. The rate of asexual reproduction is usually accepted by protozoölogists as a measure of the vitality of a strain. Woodruff (1926) carried on a pedigree culture of *Paramecium aurelia* derived from a single "wild" individual for 19 years, during which about 11,700 generations occurred without the intervention of fertilization (conjugation) and without loss of vitality, although an internal reorganization, named endomixis, was found to take place. That malarial organisms may likewise reproduce without the intervention of a fertilization process and without loss of vitality is indicated by our data (Hegner, 1926). Taliaferro (1925) found the asexual cycle of the Whitmore strain of bird malaria to be about 30 hours. This strain, as noted above, was obtained from an English sparrow in August 1913 and has been passed from bird to bird by blood inoculation ever since. This period consisted of about 131,400 hours. Dividing

this number by 30 gives 4,380, which is approximately the number of asexual generations this strain passed through without the intervention of sexual reproduction.

If we accept twenty-four hours as the length of the asexual cycle in the Hartman strain the data are as follows: total period, about 4 years; number of days, about 1460; number of asexual generations, about 1460. Whitmore reported, in 1921, that three of his canaries remained infected with the Whitmore strain for 29 months (until their death) after they were inoculated—a period during which about 700 asexual generations must have taken place in a single host. Mazza (1924) records a bird that was still infective 4 years and 2 months after the original inoculation, but the number of asexual generations cannot be computed in this case because the length of the asexual cycle is unknown for his strain.

The length of the asexual cycle for the organisms of human malaria was noted above. It seems certain that asexual reproduction continues at the same rate throughout human infections as it does in those of birds, hence the number of asexual generations may be calculated approximately by dividing the number of days of the infection by the length of the asexual cycle of the species concerned. It is of course necessary to prove that the infection measured is due to one group of parasites and not to sporozoites inoculated by mosquitoes subsequent to the original infection.

Besides the rate of asexual reproduction another criterion of vitality exists among parasitic protozoa and that is virulence. The evidence shows that both the Whitmore and Hartman strains have maintained their virulence throughout the entire period since they were secured. A factor of interest in regard to the rate of reproduction and virulence observed is the constant environment in which the malarial organisms live.

Does reorganization take place during asexual reproduction in these organisms? This is a question that can not be answered. No such phenomenon is known, but this does not prove that a reorganization process is absent, since we know very few of the cytological details of the malarial parasites during reproduction. We do know that a differentiation takes place in the blood, resulting in the production of sexual cells from the asexual generation, but as stated above these sexual cells do not continue development in the blood. Perhaps other changes corresponding to endomixis occur at some stage during the growth of the schizonts or when the merozoites are formed.

GROWTH OF TROPHOZOITES

The synchronicity of the growth and reproduction of the malarial parasites is a truly remarkable phenomenon. It is not surprising that a group of sporozoites when inoculated into the blood of a vertebrate host by a mosquito should grow to full size and undergo schizogony at approximately the same time, but it is certainly astonishing to find this still going on after a strain has been maintained continuously in canaries by blood inoculation for 11 years (Taliaferro, 1925). The synchronous growth of the trophozoites of *P. cathemerium* is illustrated in figure 7, which shows, by means of camera lucida drawings, the sizes of the parasites at 4 hour intervals during one asexual generation. Some of the schizonts produce merozoites earlier than the others and some lag behind, but most of them segment at approximately the same time day after day. The variation in growth stages in the Whitmore strain, which was 11 years old, was found by Taliaferro (1925)

to be only slightly greater than that of *P. cathemerium*, which had been passed through canaries for only a few months.

microns of 20 parasites taken from a bird at intervals of one hour for a period of 20 hours were obtained as described above.

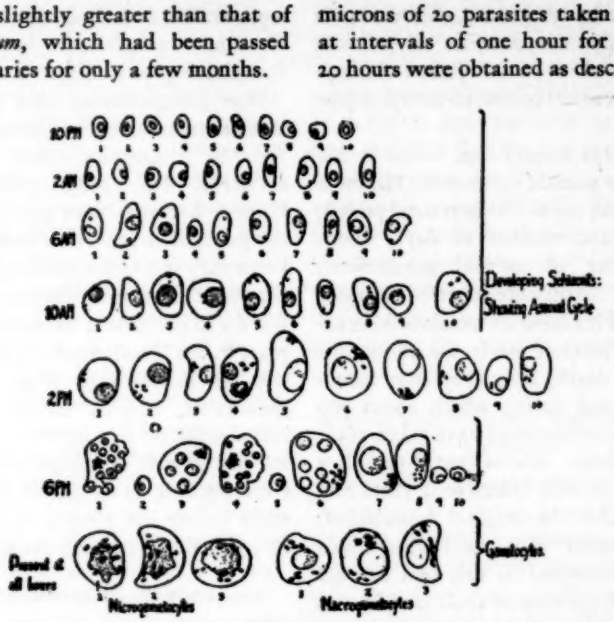


FIG. 7. REPRESENTATION OF THE CYCLE OF REPRODUCTION IN BIRD MALARIA SHOWING CHANGES IN SIZE AND VARIABILITY

Outlines of the asexual stages (× 1500) of the parasites (ten of each), showing nuclei and pigment granules, made at four-hour intervals during a consecutive period of 24 hours. In addition, outlines of three microgametocytes and three macrogametocytes, which occur in small numbers at all hours throughout the infection. The red cells in which the parasites were found have been omitted. (After L. G. Taliaferro.)

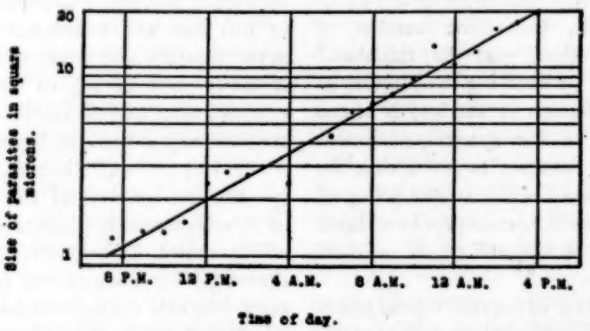


FIG. 8. GRAPH SHOWING THE GROWTH OF THE SCHIZONTS OF BIRD MALARIA (P. CATHEMERIUM), AS INDICATED BY MEASUREMENTS IN SQUARE MICRONS, DURING A 24-HOUR PERIOD (ASEXUAL GENERATION)
(After Hartman)

The growth of the trophozoites of *P. cathemerium* was studied by Hartman (1927a). The average areas in square

These measurements when plotted on semilogarithmic graph paper show that the rate of growth is constant throughout

the asexual cycle (fig. 8). "It is possible that this growth period may fit that part of an autocatalytic growth curve which can be approximately fitted with an exponential curve." (Hartman, 1927a, p. 431).

number of parasites per 10,000 red cells. Figure 9 presents the data for one bird. Average measurements were obtained as before from parasites taken at 3:00 P.M. on 8 successive days during an acute infec-

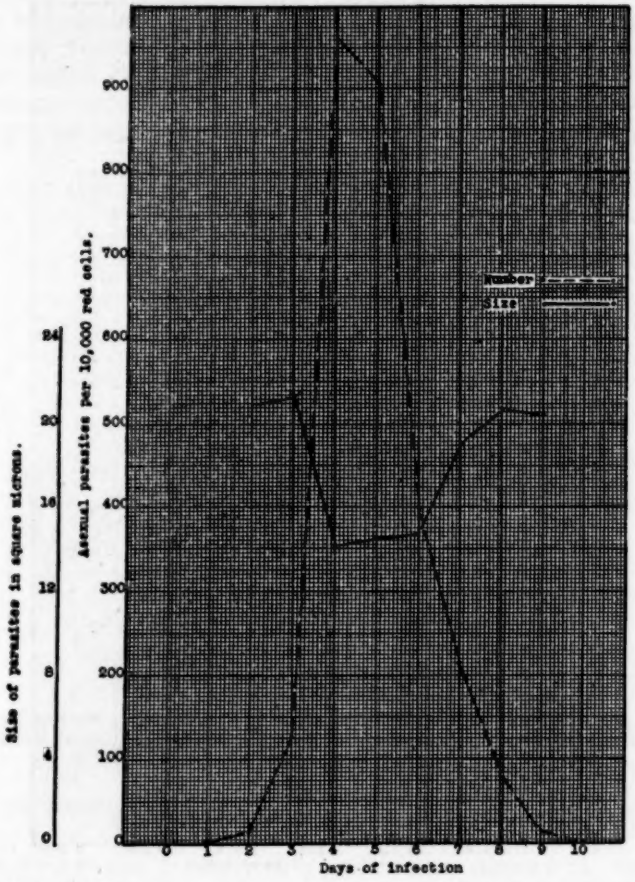


FIG. 9. GRAPH SHOWING THE DECREASE IN SIZE OF BIRD MALARIAL PARASITES AS THE NUMBER PER 10,000 RED CELLS INCREASED AND SUBSEQUENT INCREASE IN SIZE AS THE NUMBER PER 10,000 RED CELLS DECREASED (After Hartman)

Studies by Hartman of the growth of trophozoites at different periods during the course of an acute infection with *P. cathemerium* have also brought out an interesting correlation between size and

tion. The curves show a conspicuous decrease in size as the number of parasites increased to the peak and an increase in size again as the number of parasites decreased. Comparisons of the size of

the trophozoites at the beginning of the infection and at the peak in at least 20 other cases confirmed these results. The factors responsible for this phenomenon are not known.

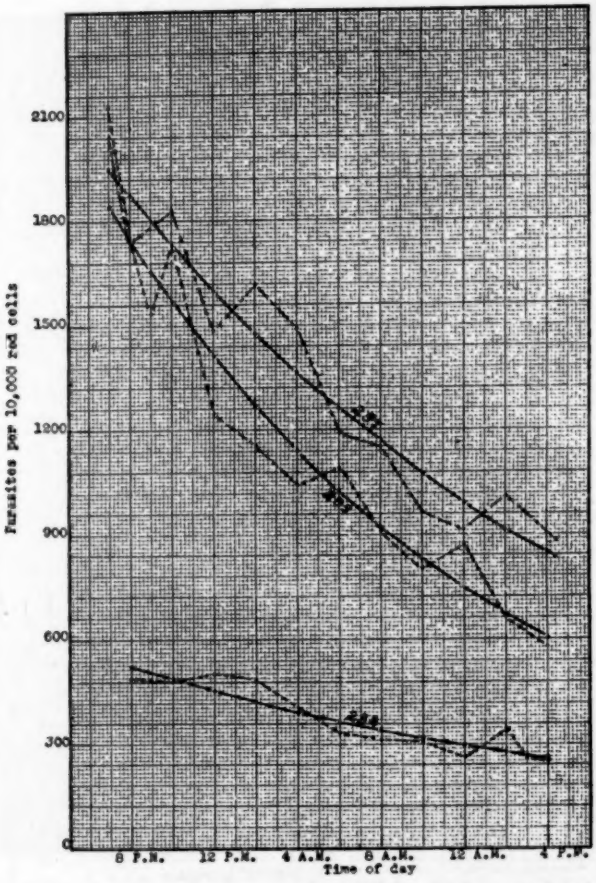


FIG. 10. GRAPH SHOWING THE DECREASE IN NUMBERS OF MALARIAL PARASITES PER 10,000 RED CELLS IN BIRDS 203, 282 AND 297 DURING A PERIOD OF 24 HOURS (ASEXUAL GENERATION)
(After Hartman)

MORTALITY DURING THE ASEXUAL CYCLE

The increase in the number of parasites during a single asexual generation and during the period of rise depends on various factors. In the first place different species of malarial parasites produce different numbers of merozoites at the end of each asexual cycle. Thus of the human tertian parasite, *P. vivax*, a single schizont may give rise to from 15 to 24, of the quartan parasite, *P. malariae*, to from 6 to 12, and of the estivoautumnal parasite, *P. falciparum*, to 8 to 10 or more. In the Hartman strain of bird malaria,

P. cathemerium, the number of merozoites per schizont, according to Taliaferro (1925), ranges from 10 to 20 with 16 as the mode and 15.5 ± 0.11 the mean. If all of the merozoites produced were to succeed in penetrating fresh red cells, in developing into schizonts and in reproducing, the number of parasites present at the end of each asexual generation would be on the average 15.5 times that of the preceding generation. A certain percentage must be deducted from the mean number 15.5 to account for those merozoites that develop into gametocytes, a number estimated by Taliaferro as 3 per cent, thus bringing the mean down to 15.03. Counts, however, prove that no such increase occurs, but that in each succeeding asexual generation there are from 5.05 to 8.96 times as many parasites as in the preceding generation. These data indicate, therefore, that from 6.07 to 9.98 of the 15.03 merozoites perish in each asexual generation during the period of rise of an acute infection.

This enormous mortality of parasites is most easily accounted for by assuming that many of the newly liberated merozoites are phagocytized, or killed by the blood serum, or fail to penetrate fresh red cells, but Hartman (1927a), by making counts at intervals of one or two hours during the asexual cycle, showed that the mortality is constant throughout the period. The results obtained from infections in 3 canaries are plotted in figure 10 with the solid lines representing the computed numbers and the dotted lines the observed numbers of parasites at intervals of one or two hours. It is obvious that there is a constant mortality rate during a single asexual cycle and not simply a mass destruction at the time merozoites are formed. This mortality rate is a mathematical constant, since the data fit approximately an exponential curve.

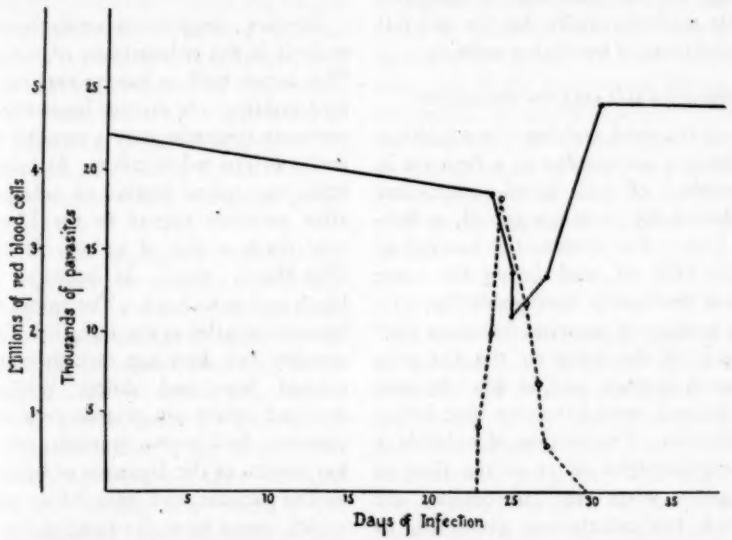


FIG. 11. CURVES SHOWING A DECREASE IN THE NUMBER OF RED CELLS (SOLID LINE) DURING THE PREPATENT PERIOD (1ST TO 23RD DAY) AND ACUTE PERIOD (23RD TO 25TH DAY) AND SUBSEQUENT INCREASE ABOVE NORMAL (After Ben-Harel)

Apparently then parasites of all ages perish during the asexual cycle, not only merozoites before they penetrate the red cells but also young trophozoites and older schizonts. The natural death of red cells and the disintegration of red cells due to the penetration of the parasites may account for at least a part of this destruction. On the other hand other problematical factors may be in operation since, as Hartman points out, the increases and decreases in the numbers of parasites resemble mathematically the rise and fall of a population of free-living animals.

EFFECTS OF MALARIA ON THE BLOOD

One of the most striking characteristics of malaria is anemia due to a decrease in the number of red blood corpuscles. Even during the prepatent period, as Ben-Harel (1923) has shown, the number of red cells falls off, and during the acute infection the loss is very great (fig. 11). As the number of parasites decreases after the peak of the infection the red cells increase in number, and, at least in some cases, become more numerous than before the infection. Destruction of red cells is obviously brought about at the time of schizogony when the merozoites are liberated, but calculations show this to be insufficient to account for the number destroyed. Parasitized red cells may also disintegrate during the growth of the schizonts but to what extent is unknown. It has been suggested that toxins produced by the parasites are capable of hemolyzing red cells that are not parasitized (Celli, Carducci and Casagrandi, 1902, 1903). Boyd (1925) tested this idea by subjecting normal red cells to the action of serum from infected birds at a temperature normal to the canary, but without any evidence of hemolysis. Phagocytosis has also been suggested but little supporting data are available.

That there is an attempt within the bird to replace the red cells that are destroyed is indicated by the increased activity of the blood-forming organs during the infection and the increased number of young red cells that appear in the circulation. During the subpatent period the blood regains the normal number of red cells and continues in this condition unless disturbed again by a relapse.

EFFECTS OF MALARIA ON THE SPLEEN

Another conspicuous characteristic of malaria is the enlargement of the spleen. This occurs both in human malaria and in bird malaria. In normal birds the spleen measures approximately 3 mm. by 2 mm., and is bright red in color. In parasitized birds the spleen begins to enlarge soon after parasites appear in the blood and may reach a size of 15 mm. by 5 mm. (Ben-Harel, 1923). It becomes almost black and quite hard. The spleen usually becomes smaller as the infection lessens in severity but does not quickly regain its normal size and color. Within the enlarged spleen are present two types of pigment, dark brown pigment, which is a by-product of the digestion of hemoglobin by the parasite, and light brown pigment, which comes from the hemoglobin that is liberated when the red cells break down. The lumina of the splenic capillaries contain large numbers of parasitized red cells, and also phagocytized parasites and the debris of destroyed red cells. Other characteristics of the spleen of parasitized birds are the destruction of endothelial cells, an increase in the number of large mononuclear cells, and the presence of young parasites either free or attached to mononuclear cells. The asexual reproduction of malarial parasites was observed by Ben-Harel (1923) in the spleens of birds that were examined from 2 weeks to 6 months after the end of the acute infection.

RESISTANCE OF THE HOST

The term resistance is used here for any condition in the parasite's environment within the host that is detrimental to the parasite. This resistance, as noted above, may be either natural or acquired, natural resistance referring to adverse conditions present at the time of the original invasion and acquired resistance to adverse conditions built up by the host during the course of the infection. Since the length of the asexual cycle of the bird malarial organisms is known and is constant, and also the average number of merozoites produced by each schizont, it is possible to use the numbers of parasites present at any time during a carefully followed infection as a measure of the resistance developed by the host.

If all of the parasites produced by asexual reproduction were to live and in turn reproduce, the number of parasites present in a host would increase on the average about 15 times every 24 hours (in *P. cathemerium* in which the asexual cycle is one day in length). This would continue until so many of the red cells had been parasitized that the death of the bird would occur. During the course of the infection, however, over one-half of the parasites perish during each asexual cycle and enormous numbers are destroyed at and following the peak of the infection. This destruction continues until no more parasites are to be found by ordinary routine methods in the peripheral blood and continues during the subpatent (latent) periods and during periods of relapse, since it has been shown that reproduction continues at the same rate during the entire course of the infection. The constant mortality of parasites during the asexual generations is probably due to the natural resistance of the host, such as phagocytosis, toxicity of the blood serum, death of parasitized red cells, and resistance of the red cells to the penetration of merozoites. The greater mortality of parasites at and after the peak is probably due, on the other hand, to resistance acquired by the host. The immunological basis for this resistance is unknown. During the subpatent (latent) periods the bird is in the carrier condition, that is, it is infected but does not exhibit symptoms. At this time parasites are being produced at the same rate as during the acute infections but most of them are destroyed in each asexual cycle. If a decrease in the resistance of the host occurs the parasites are enabled to increase rapidly in number and thus bring about a relapse. Relapses, as will be described later, may be brought about experimentally and hence the resistance of the host can be modified by known factors.

VIRULENCE OF THE PARASITE

Changes in virulence during the course of infections and of epidemics have been recorded for many pathogenic microörganisms. Boyd (1925) attempted to determine whether such changes occur in bird malarial parasites. The first experiments were designed to test virulence during the acute infection. Fifty birds were divided into 4 groups. The first were inoculated with parasites obtained from birds during the first and second days after their appearance in the blood; the second group with parasites taken on the third and fourth days; the third group with parasites taken on the fifth and sixth days; and the fourth group with parasites taken at various times during the subpatent period.

Although these data show that the average length of the prepatent period and period of rise are shortest when parasites taken from birds during the third and fourth days of an acute infection are

inoculated and that they are therefore most virulent at this time, the differences are not great and may be due to differences in the number of parasites inoculated or to individual differences in the resistance of the birds inoculated. The results may be tabulated as follows:

GROUP	PREPATENT PERIOD IN DAYS		PERIOD OF RISE IN DAYS	AVERAGE NUMBER OF PARASITES PER 10,000 RED CELLS AT PEAK
	Range	Average		
1	2–11	5.8	5.3	911
2	3–11	5.1	4.3	560
3	3–8	5.4	4.9	769
4	4–10	7.25	5.8	409

An attempt was also made by Boyd to increase the virulence of the parasites by rapid passage from bird to bird. Twenty-four birds were used. Each was inoculated with parasites from the preceding bird taken on the third day of the acute infection. The data obtained show no significant change in virulence that can be attributed to the rapid passage from bird to bird.

EFFECTS OF THE SUGAR CONTENT OF THE BLOOD ON THE COURSE OF THE INFECTION

Malarial parasites while in the body of the vertebrate host live in the blood stream, which constitutes a very constant environment. However, changes in the blood stream, advantageous or detrimental to the parasite, seem to take place since there are increases and decreases in the number of parasites at different stages of the infection. That the sugar content of the blood might be an important factor in the parasites' environment was suggested to the writer by the fact that Bass and Johns (1912) were unable to cultivate human malarial organisms in artificial media without the addition of sugar, and that they (1913) seem to have succeeded in cultivating these parasites in the blood of a diabetic without the addition of sugar. The fact that certain provocative agents, such as epinephrin, are known to bring about an increase in the sugar content of the blood is also suggestive. For these reasons Hegner and MacDougall (1926) and MacDougall (1927) studied the effects of changes in the sugar content of the blood on the course of infections in canaries with bird malaria. To increase the sugar content of the blood, one gram of glucose was dissolved in one cc. of water and one tenth of this was fed to each bird 4 times per day, at 3, 5, 7 and 9 P.M., a period during which schizogony occurs in the species of parasite studied, *Plasmodium cathemerium*. To decrease the sugar content of the blood 2 units of insulin were injected intraperitoneally daily. The results of the experiments indicate that the sugar content of the blood is an important factor in the environment of the parasite. In figure 4 are presented normal parasite curves of high, intermediate and low infections. In figure 12 are presented parasite curves from four birds that were fed sugar throughout the course of the infection. In bird 328 the number of parasites steadily increased until death occurred on the eleventh day, when 2,430 parasites per 10,000 red cells were present. The number of parasites remained high in bird 329 for several weeks, then decreased for a few days and then rose again, at which point the bird died. Bird 370 suffered three relapses in quick succession and finally died. In contrast to these are the parasite curves shown in figure 13 obtained from birds into which insulin was injected throughout the course of the infection. These curves represent all low infections and none of the birds died. From the experiments on these and many other birds it was concluded that increasing the sugar content of the blood by

feeding sugar to infected birds is favorable for the parasite, whereas decreasing the sugar content of the blood by injecting insulin into the bird is unfavorable for the parasite.

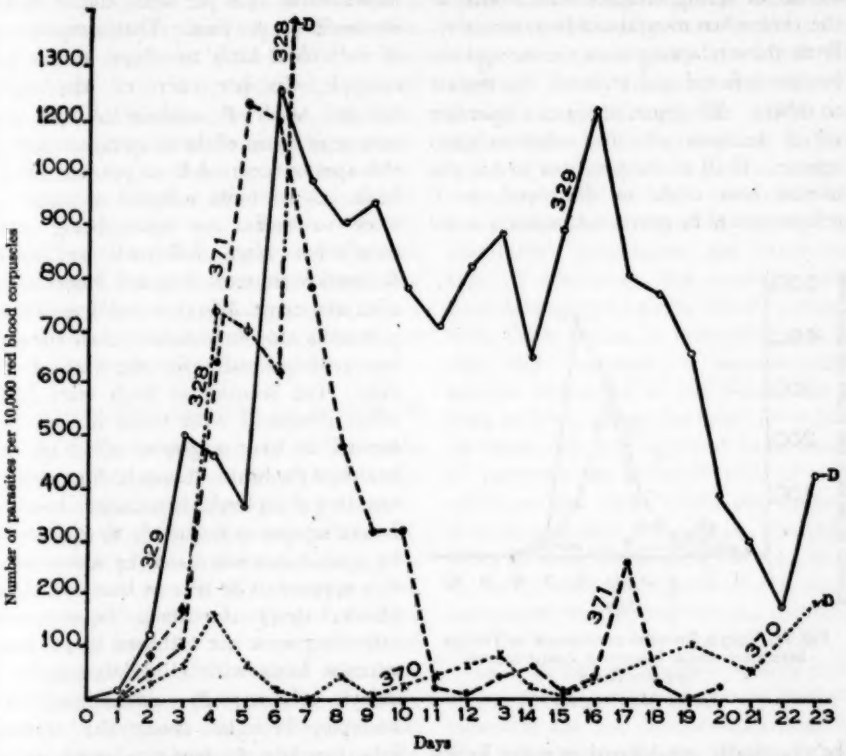


FIG. 12. CURVES SHOWING THE COURSE OF TYPICAL INFECTIONS WHEN SUGAR IS FED TO BIRDS DAILY. *D* signifies the death of the bird. *D** = death occurred on the eleventh day, when 2,430 parasites per 10,000 red cells were present. (After MacDougall.)

RELAPSE IN BIRD MALARIA

"Recovery" from an attack of malaria is usually the result of a decrease of parasites to a number insufficient to bring about symptoms; this decrease may be due to resistance acquired by the host or to treatment with quinine or some other drug. In probably most cases all of the parasites are not destroyed; a low grade infection continues until a change in the resistance of the host enables the parasites to increase to such an extent as to bring about a renewal of symptoms, a condition known as a relapse. Clinical relapses occur in about 65 per cent of infections with quartan malaria, 55 per cent with tertian malaria and 45 per cent with estivoautumnal malaria. Parasitological relapses may occur independently of clinical relapses, that is, an increase in the number of parasites may take place, as indicated by blood examination, but not great enough to induce symptoms. In certain respects relapse is the most

important of all problems in malariology. For example, in some localities malarial organisms are not carried through the winter in mosquitoes but exist only in human hosts in small numbers. With the advent of spring relapses occur, often at the time when mosquitoes become active. From these relapsing cases the mosquitoes become infected and transmit the disease to others. Thus man serves as a reservoir which becomes effective when relapses appear. If all of the parasites within the human host could be destroyed, or if relapses could be prevented, malaria could be practically annihilated in many localities.

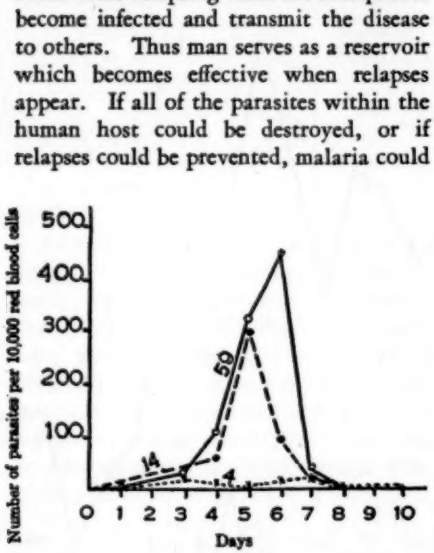


FIG. 13. CURVES SHOWING THE COURSE OF TYPICAL INFECTIONS WHEN INSULIN IS ADMINISTERED TO BIRDS DAILY
(After MacDougall)

A number of problems related to relapse have been studied by Manwell (1929), who kept accurate data of parasitological relapses for a large number of birds infected with all four of the strains maintained in this laboratory, and who also carried on certain interesting experiments. It was found that a seasonal variation in the relapse rate occurs in birds as it does in man. The greatest number of relapses were noted in the fall and winter and the smallest number in the summer. The four strains differed in their liability to relapse just as do the three species in man; the Whitmore strain relapsed in 61 per cent of the cases, *Plasmodium praecox* in 36.5 per cent, *P. inconstans* in 25.8 per cent, and *P. cathemerium* in 5.5 per cent. The susceptibility of individual birds to relapse varied; for example, 60 per cent of the birds infected with *P. cathemerium* did not relapse and most of the relapses recorded for this species occurred in 20 per cent of the birds. Some birds relapsed as many as 8 or 10 times, the result being great emaciation often followed by death. Relapses were most frequent immediately after the acute infection and least likely 3 months after inoculation; then the rate increased gradually for the rest of the year. The relapses in birds were light when compared with those of man but seemed to have a greater effect on the health of the bird. It may be that malaria resulting from blood inoculation does not induce relapse as frequently as that set up by sporozoites inoculated by mosquitoes; this appears to be true in human malaria (York, 1925). In some cases severe infections were not followed by relapses, whereas birds with mild infections had many relapses. *P. cathemerium*, for example, brought about the severest infections but the fewest relapses, resembling in this respect infections in man with *P. falciparum*.

The part played by environmental factors in bringing about relapse is problematical. Relapses in human malaria are often attributed to sudden changes in temperature, altitude, sunlight, etc., but canaries can be maintained under fairly constant conditions. High temperature and high humidity combined seemed to be a factor in the relapses recorded by Manwell, but exposure to direct sunlight had no apparent effect.

Those who believe that the human malarial parasites all belong to one species find support in the fact that sometimes an individual will undergo a tertian relapse in the spring followed by an estivo-autumnal relapse in the fall. This is presented as evidence that the tertian parasites transform into estivoautumnal parasites, both being different stages of one species of organism. Data obtained from the study of bird malaria support the view that the three species named by Hartman, as well as the Whitmore strain, are distinct species and not different manifestations of one species. Manwell has found that in infections with any one of these four strains the parasites retain their characteristics throughout the relapse period as well as the acute period.

BIRD MALARIAL PARASITES IN MOSQUITOES

Human malaria is transmitted by certain species of mosquitoes belonging to the genus *Anopheles;* mosquitoes belonging to other genera are all non-susceptible. On the other hand no species of the genus *Anopheles* are capable of transmitting bird malaria. Very little work has been done in recent years on the susceptibility of mosquitoes to bird malarial parasites. Huff (1927) lists three species of *Culex*, three of *Aedes* and one of *Theobaldia* that were known to be susceptible up to the year 1927. To this number Huff adds two more species of *Culex* and confirms previous positive results with two species of *Culex* and one of *Aedes*. He obtained negative results with five species of *Aedes*, one species of *Psorophora* and one species of *Anopheles*. In most cases suceptible mosquitoes became infected by all three species of bird malaria parasites.

The work of Huff on the fate of malarial organisms within the stomach of various species of mosquitoes has an important bearing on the problem of susceptibility and resistance to infection by these insects. The general impression among malariologists is that in susceptible mosquitoes asexual stages are killed and digested but gametocytes are stimulated to continue their development, whereas in non-susceptible mosquitoes both asexual stages and gametocytes are killed and digested. Huff, however, finds that although asexual stages are killed and digested in about 5 or 6 hours in both types of mosquitoes the gametocytes are stimulated, also in both susceptible and non-susceptible mosquitoes, to undergo maturation, fertilization and the formation of oökinetes. For example, oökinetes first appeared at the end of 12 hours in both *Culex pipiens*, a susceptible species, and *Aedes sollicitans*, a non-susceptible species, remaining in the former for at least 39 hours and in the latter for at least 20 hours, but they appeared to be unable to penetrate the stomach wall of *Aedes sollicitans* and hence could not continue their development into oöcysts. Susceptibility to infection is therefore not the result of differences in digestion but is due to some unknown reaction between oökinetes and the tissues of the stomach wall.

That differences in susceptibility exist among the individuals of a single species of mosquito has also been demonstrated by Huff. For example, one group of *Culex pipiens* mosquitoes were fed on a bird containing 1,213 parasites per 10,000 red blood cells, of which 37 per cent were gametocytes. Although every one of these mosquitoes must have ingested from 80,000 to 100,000 gametocytes only 7 of a total number of 15 that were dissected were found to have become infected. Apparently this result was due to differences in the individual mosquitoes; those that did not become infected possessed individual immunity. The basis for this immunity is unknown.

LIST OF LITERATURE

Bass, C. C., and Johns, Foster M. 1912. The cultivation of malarial plasmodia (*Plasmodium vivax* and *Plasmodium falciparum*) in vitro. Journ. Exp. Med., 16: 567–569.

———. 1913. Cultivation of malaria plasmodia (*Plasmodium falciparum*) in vitro in the blood of a diabetic without the addition of dextrose. Amer. Journ. Trop. Dis., 1: 240–249.

Ben-Harel, S. 1923. Studies on bird malaria in relation to the mechanism of relapse. Amer. Journ. Hyg., 3: 652–685.

Boyd, G. H. 1925. The influence of certain experimental factors upon the course of infections with *Plasmodium praecox*. Amer. Journ. Hyg., 5: 818–838.

———. 1926. Therapeutic action of quinine hydrochloride and certain quinine derivatives in experimental infections with *Plasmodium praecox*. Amer. Journ. Hyg., 6: 173–195.

Celli, Carducci, and Casagrandi. 1902. Primi tentavi di ricera di una emolisina nella malaria. Atti della societa per gli studi della malaria, 3: 146–157.

———. 1903. Ulteriori tentavi per la ricerca di una emolisina e primi tentavi per la ricerca di una globulina nella infezione da malaria. Ibid., 4: 59–71.

De Langen, C. D. 1925. Studies concerning the relation of the malarial parasite to the erythrocyte. Trans. Sixth Cong. F. E. A. T. M., 2: 17–25.

Derneky, K., and Hegner, R. W. 1926. Periodicity in bird malaria. Amer. Journ. Hyg., 6: 312–314.

Hartman, E. 1927a. Certain interrelations between *Plasmodium praecox* and its host. Amer. Journ. Hyg., 7: 407–432.

———. 1927b. Three species of bird malaria, *Plasmodium praecox*, *P. cathemerium*, n. sp., and *P. inconstans*, n. sp. Arch. Protist., 69:1–7.

Hegner, R. W. 1925. Medical research in malaria. Southern Med. Journ., 18: 438–440.

———. 1926. Studies on bird malaria. Southern Med. Journ., 19: 377–381.

———. 1926. A sexual reproduction without loss of vitality in malarial organisms. Science, 63: 479–480.

Hegner, Robert. 1927. Host-Parasite Relations between Man and His Intestinal Protozoa. 231 pp. New York.

Hegner, R. W., and MacDougall, M. S. 1926. Modifying the course of infections with bird malaria by changing the sugar content of the blood. Amer. Journ. Hyg., 6: 602–609.

Hegner, Robert, and Manwell, R. D. 1927. The effects of plasmochin on bird malaria. Amer. Journ. Trop. Med., 7: 279–285.

Hegner, Robert, Shaw, Edwin H. Jr., and Manwell, Reginald D. 1928. Methods and results of experiments on the effects of drugs on bird malaria. Amer. Journ. Hyg., 8: 564–582.

Huff, C. G. 1927. Studies on the infectivity of plasmodia of birds for mosquitoes, etc. Amer. Journ. Hyg., 7: 706–734.

Lawson, M. R. 1919. Crescentic bodies in estivo-autumnal malaria, their migration and attachment to the surface of the red corpuscle. Journ. Exper. Med., 31: 201–208.

MacCallum, W. G. 1897. On the flagellated form of the malarial parasite. Lancet, 2: 1240.

MacDougall, M. S. 1927. The effect of changes in the sugar content of the blood on bird malaria. Amer. Journ. Hyg., 7: 635–647.

Manwell, R. D. 1929. Relapse in bird malaria. Amer. Journ. Hyg., (In Press).

Mazza, S. 1914. On the duration of relative immunity in malaria of birds. Journ. Trop. Med. and Hyg., 27: 98–99.

Ratcliffe, H. L. 1927. The relation of *Plasmodium vivax* and *Plasmodium praecox* to the red blood cells of their respective hosts as determined by sections of the blood cells. Amer. Journ. Trop. Med., 7: 383–388.

Roehl, W. 1926. Die Wirkung des Plasmochins auf die Vogelmalaria. Arch. f. Schiffs- u. Tropen-Hyg., 30: 11–18.

Ross, R. 1898. Report on the cultivation of Proteosoma, Labbé, in grey mosquitoes, Indian Med., Gaz., 33: 401, 448.

Sinton, J. A. 1922. The situation of the malarial parasite in relation to the red blood corpuscle. Indian Med. Gaz., 57: 367–369.

Shaw, Edwin H. Jr. 1928. The absorption of chemical compounds by red blood corpuscles and its therapeutic significance in the treatment of malaria. Amer. Journ. Hyg., 8: 583–603.

Taliaferro, L. G. 1925. Infection and resistance in bird malaria with special reference to periodicity and rate of reproduction of the parasite. Amer. Journ. Hyg., 5: 742–789.

Whitmore, E. R. 1918. Observations on bird malaria and the pathogenesis of relapse in human malaria. Johns Hopkins Hospital Bull., 24: 62–67.

———. 1922. Action of light in the production of relapse in malaria. Trans. Amer. Soc. Trop. Med., (1922): 475–485.

Woodruff, L. L. 1926. Eleven thousand generations of *Paramecium*. Quart. Rev. Biol., 1: 436–438.

Yorke, W. 1925. Further observations on malaria made during treatment of general paralysis. Trans. Roy. Soc. Trop. Med. and Hyg., 1925: 108–122.

MENDELIAN INHERITANCE IN FISH

By H. B. GOODRICH

Wesleyan University and the Marine Biological Laboratory

FISH have until recently received scant attention from geneticists. Yet the relatively few studies thus far made show that they offer favorable material for such work and are likely to prove especially useful in problems of the relation between the genes and the processes of development. Fish often show brilliant color patterns that are easy to follow in inheritance or in embryonic development. Certain aquarium fish attain sexual maturity in periods less than a year, making them comparable with the rodents in rapidity of breeding.

There are, however, two principal limitations of fish for these purposes, the difficulties of cytological studies of their chromosomes and the high mortality of young fish, which is likely to prevent careful studies of strength of linkage and frequency of cross-overs.

Various independent lines of investigation are converging to give information bearing on genetic work with fish. First there have been the observations of field naturalists and systematists, who have shown that certain groups of fish appear to be far more variable than others; secondly those of the aquarists, especially the German aquarists, who through the medium of their principal Journals, the *Blätter für Aquarien und Terrarienkunde* and the *Wochenschrift für Aquarien und Terrarienkunde* have accumulated information in regard to the characteristics, care and possibilities of scientific investigation of aquarium fish. The scientific work in government and commercial fish hatcheries has also been an aid, and finally the professional zoologists and geneticists are beginning to utilize fish in their investigations.

The writer wishes to make acknowledgment of the usefulness of Bashford Dean's *Bibliography of Fishes* as a guide to the earlier literature and to the kindness of Dr. E. W. Gudger, who has made fully available the continuation of this Bibliography, which is maintained in card catalog form at the American Museum of Natural History, New York City.

CLASSIFICATION OF FISH UTILIZED IN GENETIC INVESTIGATIONS

The following outline classification (based on Jordan, 1923) indicates the position of the various genera of fish that have thus far been utilized in genetic investigations and that are reviewed in this paper.

Super Order Teleostei
- Order Eventognathi
  - Family 237 Cyprinidae
    - Genus *Carassius*
      - Species *C. auratus*
- Order Cyprinodontes
  - Family 290 Cyprinodontidae (Killifishes)
    - Genus *Oryzias*
      - Species *O. latipes*
    - Genus *Lebistes*
      - Species *L. reticulatus*
    - Genus *Rivulus*
      - Species *R. urophtalmus*

Family 294 Poeciliidae
(Top minnows)
Genus *Platypoecilus*
Species *P. maculatus*
Genus *Xiphophorus*
Species *X. helleri*
(*Lebistes* is included in family Poeciliidae by Regan, 1913)

LEBISTES

Lebistes, which is popularly known as the "Millions fish" and the "Guppy," is native in Venezuela, Trinidad, the Barbadoes, and has been introduced as a means of mosquito control in many localities such as Guiana, Panama, Jamaica, South Africa, etc. Since its first description as *Poecilia reticulata* by Peters in 1859, it has been assigned to various genera, *Girardinus*, *Acanthophacelus*, and is now best known as *Lebistes reticulatus* (Regan, 1913). It seems to have first appeared in Germany as an aquarium fish about 1905 (Wichand, 1906).

Lebistes has been shown by the work of Schmidt, of Winge and of Blacher to be remarkably adapted for genetic investigations. The color pattern is exceedingly variable in the males, and there is a rapid development so that sexual maturity is reached in from three to four months. There exists a striking dimorphism of sex. The female measures about 5 cm. in length and the male but 2.5 cm. The female is nearly uniformly pigmented—an olive brown color—while the male shows brilliant hues in varied combinations. This fish is viviparous, and the period of pregnancy is about thirty days. Details of the care of the fish are given by Winge (1927).

The first paper (Schmidt, 1920) dealing with the genetics of *Lebistes* revealed the existence of Y-chromosome inheritance, appearing only in males and transmitted only by males. A succession of later papers (Winge, 1922 b, 1923, 1927) have reported altogether the discovery of eighteen genes, of which only one is autosomal or non sex linked and seventeen are sex linked. Of these seventeen nine have thus far been restricted to the *Y* chromosome and three to the *X* chromosome, while five have been found to cross over between the *X* and *Y* chromosomes. This list has been modified by Blacher (1927, 1928) by subdividing two of Winge's genes into two and four genes respectively and adding one new gene. It should be borne in mind that the female, except in a few cases of sex reversal in old age (Winge, 1927; Blacher, 1926a and b), never exhibits the colors. She is known to transmit the color by progeny tests. The names and symbols of these genes are listed in table 1, and in figure 1 are shown in diagramatic form the color patterns of genes minutus, sanguineus, coccineus and vitellinus separately and in combination. In the original papers the patterns of all heritable characters are reproduced in color, and these must necessarily be consulted by anyone utilizing this type for genetic studies.

One notable result of these investigations and also of Aida's work on *Oryzias* has been the discovery of crossing over between the *X* and *Y* chromosomes. This is most clearly illustrated by the relationship of the genes maculatus and elongatus as described by Winge (1923). Maculatus is restricted to the *Y* chromosome and phenotypically it exhibits a black spot on the dorsal fin, a red spot below and in front of the same fin and a black spot (not always developed) in the anal region (fig. 2). Elongatus produces an elongation and a reddish yellow color on the dorsal and ventral edges of the caudal fin (fig. 2). As illustrated by figures 2 and 3 the gene *e* appears to cross from the *X* chromosome to the *Y* chromosome, which already contained gene *m*,

TABLE 1

TERMS AS GIVEN BY WINGE		ADDITIONS AND MODIFICATIONS BY BLACHER	NATURE OF PHENOTYPE	MODE OF INHERITANCE
Name	Symbol			
maculatus	(*ma*)		color character	*Y* chromosome
		macula rubia (*mr*)	color character	*Y* chromosome
		macula nigra dorsales (*mnd*)	color character	*Y* chromosome
iridescens	(*ir*)		color character and silver sheen of side of body	*Y* chromosome
		bimaculatus (*bi*)	color character	*Y* chromosome and allelomorphic to *ru* complex (Blacher)
		variabilis—apparently not homologous with variabilis of Winge—causes yellow color in dorsal region of caudal fin (*va*)	color character	*Y* chromosome and allelomorphic to *ru* complex (Blacher)
		macula caudales (*mc*)	color character	*Y* chromosome and allelomorphic to *ru* complex (Blacher)
		anterior rubra (*ar*)	color character	*Y* chromosome and allelomorphic to *ru* complex (Blacher)
oculatus	(*oc*)		color character and form of caudal fin	*Y* chromosome
ferrugineus	(*fe*)		color character	*Y* chromosome
sanguineus (derived from ruber)	(*sa*)		color character	*Y* chromosome
aureus	(*au*)		color character and form of caudal fin	*Y* chromosome
armatus	(*ar*)	gladigerens (*g*)	color character and form of caudal fin	*Y* chromosome
		modified gladigerens (*g'*)	color character and form of caudal fin	*Y* chromosome
pauper	(*pa*)		color character	*Y* chromosome
variabilis	(*va*)		color character	*Y* chromosome
coccineus (derived from sulphureus)	(*co*)		color character	*X* chromosome
lineatus	(*li*)		color character and form of caudal fin	*X* chromosome
tigrinus	(*ti*)		color character	*X* chromosome
luteus	(*lu*)		color character	*X* and *Y* chromosomes
elongatus	(*el*)		color character and form of caudal fin	*X* and *Y* chromosomes
minutus (derived from ruber)	(*mi*)		color character	*X* and *Y* chromosomes
vitellinus (derived from sulphureus)	(*vi*)		color character	*X* and *Y* chromosomes
cinnamoneus	(*ci*)		color character	*X* and *Y* chromosomes
zebrinus	(*zt*)		color character	autosomal

thus producing chromosome *Yem* of which the inheritance may be traced. Gene *e* was also later found to cross back to an *X* chromosome. Other probable examples of crossing over have been noted, and in one case it has been a means of further analysis of the genetic complexes at first designated as genes sulphureus and ruber (Winge, 1922), which have been respectively subdivided into genes vitellinus and coccineus, and minutus and sanguineus (Winge, 1927). This was because certain portions of the color pattern of *su* and *ru* were observed to separate and cross over in inheritance. Those which showed crossing over were minutus and vitellinus, while coccineus remained associated with *X* and sanguineus with *Y*.

These investigations have raised several questions in regard to theoretical interpretation. Certain of the genes, such as sanguineus and coccineus, may be allelomorphs instead of occupying different loci in the chromosomes. The former is the type of interpretation adopted by Bellamy (1924, 1928) in his study of *Platypoecilus*, while Gordon utilizing the same material favors the concept of independent loci. Winge repeatedly refers to the *X* chromosome as being "empty," thus indicating his preference for the presence and absence hypothesis for this material. He finds no evidence that there exist active allelomorphs of the color factors and considers it possible that they may be non-existent. This concept is indicated in his formulae by the Symbol X_o. Blacher, however, (1928), considers

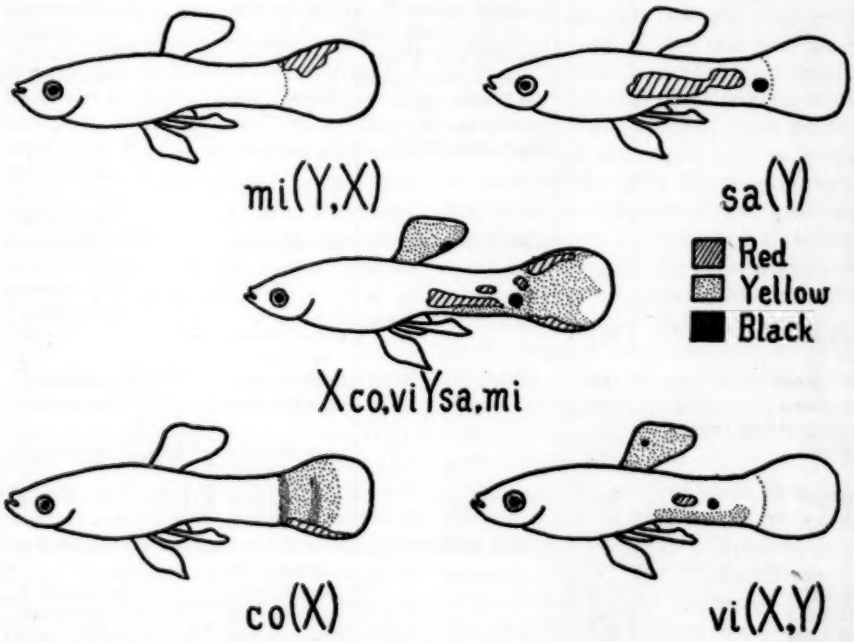


FIG. 1. COLOR EFFECTS OF GENES MINUTUS, SANGUINEUS, COCCINEUS AND VITELLINUS IN LEBISTES
Combined effect of all four genes shown in central figure. (After Winge, 1927.)

that the genes derived from Winge's iridescens complex are allelomorphic to is controlled by a single pair of genes—a dominant factor for maleness resident in

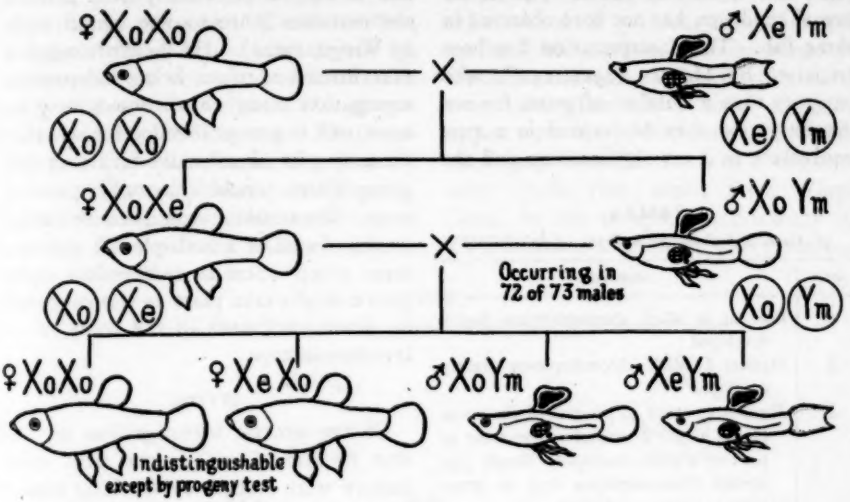


FIG. 2

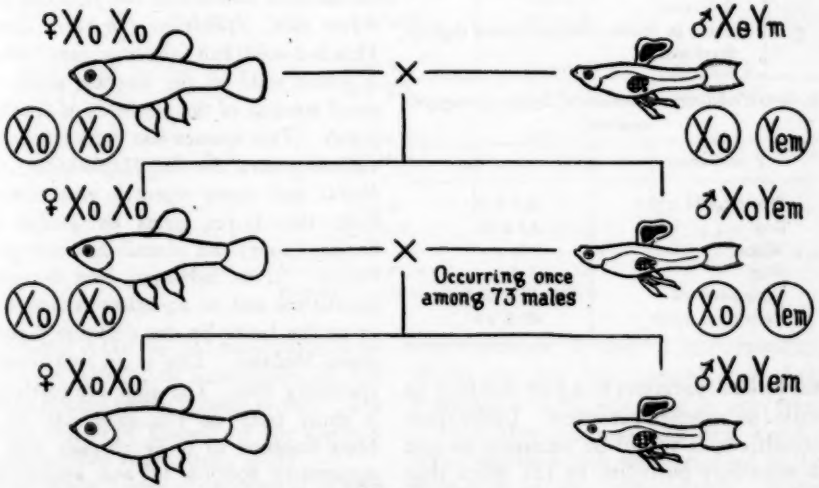


FIG. 3

FIGS. 2 AND 3. Y-CHROMOSOME INHERITANCE AND CROSSING OVER IN LEBISTES

Fig. 2 shows *Y*-chromosome inheritance without crossing over. Fig. 3 shows the effect of a cross-over. Colors: Black, solid black; red, cross hatching; yellow, stippled. (After Winge, 1923.)

the sulphureus complex. A further point emphasized by Winge is that his evidence supports the idea that sex determination the *Y* chromosome and recessive factors for femaleness present in the *X* chromosomes. He considers that if genes for maleness

and femaleness were genetic complexes of many genes crossing over would take place and intersexes result. This latter sexual condition has not been observed in these fish. This interpretation has been criticized by Morgan (1924, 1926), who suggests that a number of genes for sex determination may be located in a part equivalent to a sex chromosome and the sex linked characters in a part that may be called an attached autosome. Under these conditions it would be necessary to add a secondary postulate to the effect that crossing over might occur in the autosomal section but not in the sex chromosome part.

TABLE 2

A. Genes and phenotypes in Oryzias (Aplocheilus)

GENE	PHENOTYPE
B	Pigment in black chromatophores highly developed
b	Pigment in black chromatophores slightly developed
B'	Pigment in about 50 per cent of chromatophores highly developed and in about 50 per cent slightly developed. Deeply pigmented chromatophores tend to group forming variegated pattern.
R	Pigment in yellow chromatophores highly developed
r	Pigment in yellow chromatophores slightly developed

B. Genetic constitution of varieties of Oryzias (homozygous condition)

PHENOTYPE	GENOTYPE
Brown (wild type)	*B B R R*
Red	*b b R R*
White	*b b r r*
Blue	*B B r r*
Variegated red	*B' B' R R*
Variegated white	*B' B' r r*

Demerec (1928), considering the situation in *Lebistes* from the point of view of his studies in the frequency of mutations, has suggested that it is highly improbable that almost all mutations should be limited to one of the twenty-three pairs of chromosomes (chromosome counts made by Winge, 1922a). He therefore suggests that instead of there being independent segregation many chromosomes may be associated in groups in reduction and that there may be occasionally breaks in this group which would account for crossing over. The situation would thus be similar to that found in a multiple *XY* chromosome group where an independent segregation might take place as was suggested by Goodrich (1926) in the study of an invertebrate type.

ORYZIAS

Of the genetic investigations on fish that by Aida (1921) is the most satisfactory with respect to the large counts obtainable and consequent definite results. As material he utilized the Japanese fresh water fish, *Aplocheilus (Oryzias) latipes*. This is a small fish (about 30 mm.) which is found wild in the ditches, pools and small streams of the ricefields of Southern Japan. This species has been referred to various genera, *Poecilia*, *Haplocheilus*, *Aplocheilus* and most recently was removed from this latter genus by Jordan and Snyder (1907) and placed in a new genus *Oryzias*. It is, however, best known to geneticists and to aquarists as *Aplocheilus* or to the latter by the common Japanese name Medaka. This is an oviparous or spawning fish. The eggs are carried for a short time on the underside of the body fastened to it by threads that are apparently formed in and attached to the walls of the oviduct. This characteristic is an advantage in genetic experiments as several females of different genotype may be left with a single male in an aquarium and there is no doubt as to the source of the eggs. Details of the care of

the fish are recorded by Aida (1921) and Goodrich (1927). It appears that the normal period for attainment of sex-maturity is one year. The writer has, however, reared fish to maturity in six months, and it seems probable that by proper control of conditions two generations may be reared per year. The investigations of Aida on *Oryzias* were preceded by two less complete papers (Toyama, 1916; Ishiwara, 1917) and a reference to crossing experiments by Ishikawa (1913). This latter is the earliest publication dealing with Mendelian inheritance in fish that is known to the present writer. The species has been known to the German aquarists since 1897 (Bade, 1898).

Aida made a genetic analysis of certain color varieties—brown, red, white, variegated and blue. These he found to be due to the interaction of genes as indicated in table 2B. An inspection of these formulae show that B, B' and b form a series of multiple allelomorphs. In this series the genes are borne by autosomes, while the allelomorphic genes R and r are carried by the X and Y chromosomes. In Aida's experience an R gene was usually carried by the Y chromosome and r restricted to the X chromosomes. Hence white males were rare. The white males that did appear were the result of crossing over of the R gene from the X to the Y chromosome. Aida then shares with Winge (1922) in the independent discovery of Y-chromosome inheritance and of crossing over between X and Y chromosomes, which are the first examples of these phenomena to be described in any type.

Aida also distinguished the various types of cells which were involved in the formation of the color pattern. These observations are discussed below in connection with developmental phenomena.

Table 3 gives an example of the mode of inheritance in *Oryzias* showing a typical case of dihybridism and the interaction of factors which yields an unusual ratio.

TABLE 3

Di-hybrid cross in Oryzias showing Y chromosome inheritance and interaction of factors

Brown ♂ $B\,B\,X_RY_R$ × white ♀ $b\,b\,X_rX_r$

Brown ♂ $B\,b\,X_rY_R$ × brown ♀ $B\,b\,X_RX_r$

	$B\,Y_R$	$B\,X_r$	$b\,Y_R$	$b\,X_r$
$B\,X_R$	brown ♂ $B\,B\,X_RY_R$	brown ♀ $B\,B\,X_RX_r$	brown ♂ $B\,b\,X_RY_R$	brown ♀ $B\,b\,X_RX_r$
$B\,X_r$	brown ♂ $B\,B\,X_rY_R$	blue ♀ $B\,B\,X_rX_r$	brown ♂ $B\,b\,X_rY_R$	blue ♀ $B\,b\,X_rX_r$
$b\,X_R$	brown ♂ $B\,b\,X_RY_R$	brown ♀ $B\,b\,X_RX_r$	red ♂ $b\,b\,X_RY_R$	red ♀ $b\,b\,X_RX_r$
$b\,X_r$	brown ♂ $B\,b\,X_rY_R$	blue ♀ $B\,b\,X_rX_r$	red ♂ $b\,b\,X_rY_R$	white ♀ $b\,b\,X_rX$

Summary: Males: 6 brown, 2 red
Females: 3 brown, 3 blue, 1 red, 1 white

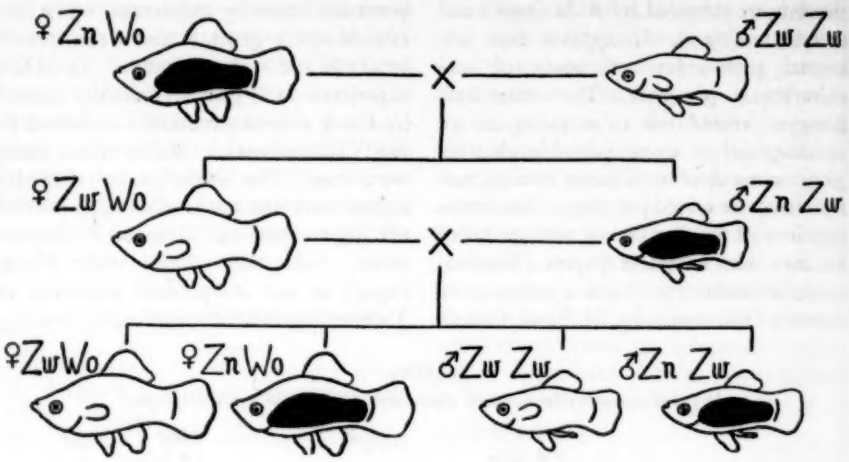


FIG. 4

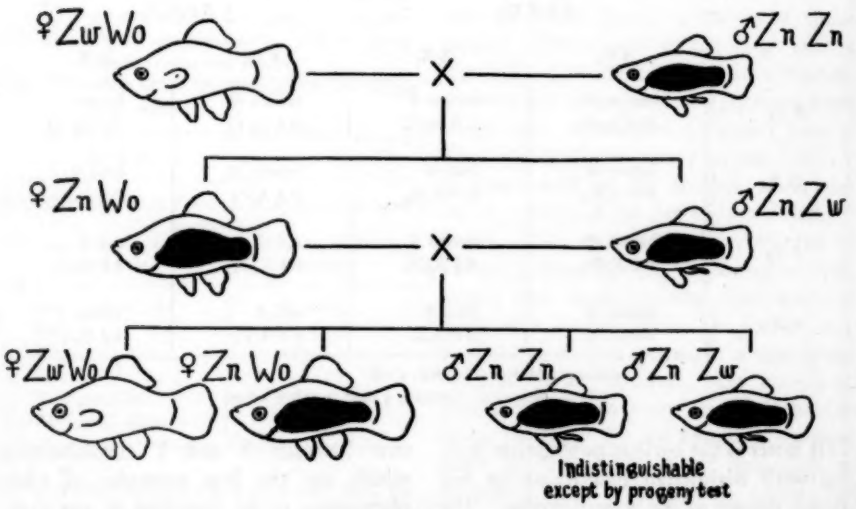


FIG. 5

FIGS. 4 AND 5. ZW INHERITANCE OF CHARACTER NIGRA IN PLATYPOECILUS

Fig. 4. Cross of Nigra female by white (Bellamy) or stippled (Gordon) male. Fig. 5. Cross of white (stippled) female by Nigra male. (After Bellamy.)

PLATYPOECILUS

Platypoecilus is a genus native in freshwater streams and bayous of southern Mexico.

The species *P. maculatus* is remarkably variable in color pattern as noted by Meek (1904) from field collections and later by the German aquarists. An outline of the taxonomic history of this type is given by Gordon (1927). This fish is viviparous, the gestation period is

about thirty days and sexual maturity of the female is attained in about eight months, but there is considerable variation. That of the attainment of male maturity is tabulated by Bellamy (1924). The color patterns have been variously named, and a list of fifteen is given by Gordon (*loc. cit.*). It is not surprising that this highly variable type should prove suitable for genetic investigations. A systematic study was first undertaken by Bellamy (1922, 1924, 1928), who has discovered sex linked characters which exhibit Abraxas or *ZW* type of inheritance in contrast to the conditions found in *Oryzias* (*Haplocheilus*) and *Lebistes*, where the Drosophila *XY* type prevails. Figures 4 and 5 illustrate the *ZW* type of inheritance. Gordon (1926, 1927) has made an independent genetic analysis of *Platypoecilus* confirming Bellamy's finding of the *ZW* type of inheritance but also adding the autosomal character stippled; he is in disagreement with Bellamy in regard to certain details. It is well to keep in mind in regard to *Platypoecilus* that the various varietal names given by systematists and aquarists should not be confused with designations of analyzed Mendelian characters. Thus the red variety, or Rubra, a red "platy," involves factors for "spots, stipples and *red*." The following table (4) is an attempt to harmonize the present nomenclature. Of the genetic factors *St* and its allelomorph *st* are autosomal, while all others are sex linked and carried by the *ZW* chromosomes. Bellamy regards these sex linked factors as constituting a series of multiple allelomorphs such that males may be homozygous or may carry any two of the genes *R*, *N*, *P*, *W*, etc., while the female, being the heterogametic sex *ZO*, will carry only one gene of the assortment. Fraser and Gordon (1928, 1929; the authors have kindly allowed the pres-

TABLE 4

Terminology of Platypoecilus

TERMINOLOGY BASED ON THAT GIVEN BY AQUARISTS	TERMINOLOGY SUGGESTED BY GORDON 1927	GENETIC SYMBOLS	
		Bellamy	Adapted from Gordon 1927
Rubra	Red-platy	*R*	*R*
Nigra	Black-platy	*N*	*N*
Pulchra	Spotted-platy	*P*	*Sp*
White (Bellamy 22)	Stippled-platy	*W*	*St*
Immaculatus	Gold-platy		*r, n, sp, st*

According to Gordon the Rubras or Red-platys of aquarists usually have other factors present, namely: RR SpSp StSt.

The Nigras or Black-platys usually have Stipples, thus: NN StSt.

The Gold-platy is a multiple recessive.

Chromatophores of Platypoecilus from Gordon (1927)

	RED	SPOTTED	BLACK	STIPPLE	GOLD
Melanophores					
a. Stipples	+	+	+	+	−
b. Spots	+	+	+++	−	−
Erythrophores	+	−	−	−	−
Xanthophores	+	+	+	+	+

ent writer to refer to their paper while in press), however, found evidence which indicates that there may be present a gene-carrying *W* chromosome into which genes may cross over from the *Z* chromosome. A second conclusion of Fraser and Gordon, based on an apparent crossover, is that genes for red color and spotting should not be considered allelomorphic but rather occupy closely adjoining loci on the paired chromosomes, so that the preferred formula for a heterozygous male is *Rsp*, *rSp* rather than *R*, *Sp*. This interpretation is followed in table 4. It is possible that further work will indicate that *N* (Nigra) should also be considered as a closely linked gene rather than as an allelomorph of *R* and *Sp*.

The color patterns in *Platypoecilus* are produced by the development of various chromatophores as indicated by the following table (4, from Gordon). It is interesting to note that here is indicated in most cases a relation between the genes and definite types of cells and in one case (Black) an effect of the arrangement or massing of the cells to produce a broad black band on either flank of the fish.

CARASSIUS

The goldfish, *Carassius auratus*, is the earliest known of ornamental fish here discussed. Chen (1925) in his review of the old Chinese literature finds that the red scaled fish were reported observed during the Tsin dynasty (265–419), but they were not domesticated until the Sung dynasty (960–1278). The taxonomic designation is now applied both to the ornamental and to the wild or brown form, which is native of China but has been elsewhere introduced.

The practice of goldfish culture is of course well understood. One of the best manuals is that of Innes (1921). (See also Fearnow, 1925). In spite of the familiarity of the goldfish and the abundance of varieties little progress has been made with any Mendelian analysis until the present year. The delay has probably been due to the necessity of more extensive facilities—outdoor pools, etc.,—and the longer time required for attainment of sexual maturity (two years is usually considered the minimum). Hance (1924) in a brief note reports the probable dominance of red and black over white, of normal tail over double or fantail and of normal eyes over the telescope variety. No ratios are reported.

Chen's paper (1928) appears to be the first Mendelian analysis that has been made. He has studied the inheritance of certain characters found in the ordinary goldfish and the "Scaleless" varieties, of which the type known to fanciers, Shubunkin, is an example. The so-called "Scaleless" types have scales, but they are transparent and hence almost invisible on account of the absence in the scales of a layer of reflecting crystals, the guanin, which gives the silvery sheen to the sides and belly of many fish. This material may be present in one or more layers—in some cases one underlying and another in the scales.

The investigations by Chen show that the scaled and "scaleless" characters are allelomorphic, and he has designated the genes as *T* (scaled) and *T'* (scaleless). Differences in development of the reflecting layer are also accompanied by characteristic pigmentation. The effect of the genes may be stated as follows: Gene *T* (homozygous) produces several layers of reflecting tissue including that in the scales, and black and yellow chromatophores are abundant. Gene *T'* (homozygous) causes a reduction of reflecting tissue until it is nearly or wholly absent. The black chromatophores are restricted to an area at the base of the caudal fin and the

yellow chromatophores are absent. The heterozygous types *TT'* reveal a condition of incomplete dominance. The reflecting tissue is present in varying degree—on the head, a portion of the deeper layer over the body, in isolated scales (from 2 to 14) or combinations of all. The black and yellow chromatophores are both present but so arranged as to give a characteristic mottled color effect—that of the Shubunkin.

It thus appears that the Shubunkin of the breeders is a heterozygous type, which it is impossible to perpetuate as a pure stock. The homozygous scaleless types are usually weaker and less abundant. If, however, this race is maintained and bred with scaled types, the Shubunkin is always produced.

RIVULUS

The form which has most recently entered the lists for genetic investigation is *Rivulus urophtalmus*. A brief note by Constantinescu (1928) indicates the dominance of a black color phase over a red phase. This pair of allelomorphs is apparently autosomal.

SPECIES HYBRIDS

Thus far the interspecific hybridization of fish has been of greater importance in the study of certain phases of the mechanism of development than in the study of inheritance. That is, such experiments have yielded results bearing on the relation of chromatin to development, of controlling factors in ratio of cleavage and in the process of gastrulation. Almost all of these crosses have been between types of which no Mendelian analysis had been made. There has, therefore, been no possibility of tracing the effects of individual genes. Since hybridization among fish has had a considerable degree of success, it seems probable that as our knowledge of Mendelian inheritance in fish increases such observations will become possible.

Two sorts of studies have been made—those dealing with the phenotypic effects of the hybridization and the studies of the behavior of chromatin in hybrids. There have been numerous accounts of hybridization or alleged fish hybrids which are of little value (see Dean, *Bibliography of Fishes*, Vol. 3, pp. 505–507 for references). The earliest of the more accurate observations were those of Appellöf (1894) and Moenkhaus (1904). The former made crosses between Cod and Flounder, Cod and the European Cunner, the Dab and Flounder, and between two species of stickleback. In some crosses development stopped at the conclusion of cleavage and in others when the embryo was fully formed. Moenkhaus crossed *Fundulus heteroclitus* and *Menidia notata*. In both of these cases there is little information bearing on the relative effect of either parent except on cleavage stages and gastrulation. The work of Moenkhaus is notable in showing that the chromosomes of both parents were present in nuclei and were fully mingled. Further studies of chromosome behavior have been made by Morris (1914), P. and G. Hertwig (1914), and Pinney (1922, 1928). A review of chromosome behavior in hybrids has been made by Morgan (1927). Bancroft (1912) has made a careful analysis of the history of chromatophores in hybrids of *Fundulus majalis* and *Fundulus heteroclitus*. He finds that certain characteristics of pigment cells in *F. heteroclitus* are dominant over the condition found in *F. majalis*, while on the other hand in regard to certain features of the time of development of chromatophores he finds a "blending" or intermediate condition. Newman in an extensive series of papers (1914, 1915, 1918) has shown the possibilities of many

teleost hybridizations. Some hatch, many do not. He describes many instances of varied effects of hybridization—dominance, blending, mosaic conditions. Essentially similar results have been obtained by Paula and Gunther Hertwig (1914) in fish from the Gulf of Naples.

Some of the most interesting cases of species hybrids of fish have been discovered by the aquarists. The best known of these are the crosses between *Xiphophorus belleri* and the varieties of *Platypoecilus maculatus*. Most matings have been between *Xiphophorus* female and *Platypoecilus* male. In many respects the hybrids are intermediate between the parental types. In regard to coloration there is some evidence of segregation. This is summarized in table 5. It is possible to tentatively harmonize these somewhat diverse results by assuming that in crosses (2) and (4) *Platypoecilus* was heterozygous for factors affecting melanophore development, in (1) and (3) homo-

TABLE 5

Xiphophorus belleri (strigatus) × *Platypoecilus maculatus*

Inheritance of coloration

			HYBRID CHARACTERS	
			Male	Female
(1) Gerschler (1914)				
X. strigatus female	×	*P. maculatus* male	Xiphophorus characters	Xiphophorus characters
(2) Kosswig (1928)				
X. belleri female	×	*P. maculatus* male var. black platy	57 black 25 red	5 black 42 red
			(total 62 black 67 red)	
(3) *X. belleri* female	×	*P. maculatus* male (gold platy)	21 red	17 red
(4) *X. belleri* female	×	*P. maculatus* male (red platy)	28 red with black flecks 22 black (sex not determined)	
(5) Innes (1921)				
X. belleri female	×	*P. maculatus* male (red platy)	Red, black splotches both sexes	
(6) Kissel. Reported by Mellon (1928)				
X. belleri female	×	*P. maculatus* male (red platy)	1 red male, 49 mottled (black splotches?) both sexes	
(7) Haffner (1913). Reviewed by Gerschler (1914)				
P. maculatus female	×	*X. belleri* male	Platypoecilus characters	Xiphophorus characters

zygous for absence of Nigra and spotting, and in (5) homozygous for spotting. The most striking result is that obtained by a backcross from the F_1 (5) with *Xiphophorus helleri* male. This gives a vigorous hybrid larger than either parent and having a brilliant red color. (See Innes, 1921, pp. 68–69; and Mellon, pp. 89–90). It may be that genes which affect the red chromatophores have been received from both parent species.

Various crosses have been made by the aquarists. See Schreitmüller, 1925 (*Danio rerio* × *Danio albolineatus*), 1926a (*Xiphophorus helleri* female × *Lebistes reticulatus* male, *Xiphophorus helleri* female × *Mollienesia formosa* male, *X. helleri* male × *Mollienesia velifera* female, *X. helleri* female × *Limia arnoldi* male, *Xiphophorus helleri* female × *Limia nigrofasciata* male, *Xiphophorus helleri* female × *Phalloceros caudomaculatus*), Schreitmüller, 1926b (*Brachydania rerio* × *Danio malabaricus*), Schreitmüller, 1926c (*Gambusia holbrooki* female × *Cnesterocdon decemmaculatus* male), Meinken, 1925 (*Danio albolineatus* male × *Danio analipunctatus* female). These papers give but brief descriptions of the experiments but they are suggestive of the possibilities for more critical analysis. Embody (1918) has described hybrids obtained by artificial insemination between pike and pickerel and Phillipps (1922) gives an account of crosses between two species of salmon from Australia. These reports seem to indicate that fish are more favorable than most other animal forms for this type of experimentation.

SEX DETERMINATION AND SEX DIFFERENTIATION

The phenomena of sex determination and sex differentiation are essentially one part of the larger problem of the relationships between the genes and the physiology of development. It is a part, however, which has thus far been more completely analyzed and in which the complexities of the situation are most clearly revealed. It seems probable that studies on fish may yield data of importance bearing on these problems. The fact that both *XY* and *ZW* types of inheritance are found in closely related fish such as *Lebistes* and *Oryzias*, *XY*, and *Platypoecilus*, *ZW*, is of some significance in considering the evolutionary origin of these conditions. The existence of this situation in *Lebistes* has led Winge (1923, 1927) to the opinion that there is present a single pair of genes—a recessive for femaleness borne by the *X* chromosomes and a dominant gene for maleness borne by the *Y* chromosome. This is obviously a concept sharply at variance with that held by most workers on *Drosophila*.

Harms (1926) has crossed normal females of *Xiphophorus helleri* with males that have attained their sex after reversal from the female condition. His results though limited are in accordance with the hypothesis that there exists in these types an *XY* complex and that in sex reversal the original sex formula is retained. Thus in the above cross an *XX* female is mated with an *XX* male and as expected under these conditions all offspring are female.

The work of Essenberg (1923, 1926) shows that sex reversal is normal in *Xiphophorus*. There is a great preponderance (74 per cent) of females among the young fish, but later the sex ratio is reversed, giving 75 per cent males. It is not known how widely such cases of sex reversal may occur among fish. Geiser (1924) gives a tabulation of sex-ratios among fish.

Conditions of sex reversal naturally suggest investigations of the relation of secondary-sex characteristics to the gonads. Blacher (1926) and Frazer and Gordon (1929) have noted a correlation between

testes development and appearance of male colors. The most extensive studies are those on *Gasterosteus* and *Xiphophorus*, by van Oordt (1924, 1925), who considers that there is a correlation between the development of male sex cells and secondary sex characters and that the interstitial cells of the testes play no part in internal secretion. This conclusion is in accord with that of Champy (1923) but quite the reverse of that of Courrier (1922). Very little experimental work of removal of gonads has been done. Kopec (1927) performed castration experiments on the fish *Phoxinus laevis*, after which some failed to assume the nuptial hues. They did not however live more than three weeks after the operation.

CHROMOSOMES

Fish have proved to be notably difficult material for study of chromosomes. Winge (1922a) records the haploid number of 23 from *Lebistes*. Goodrich (1927) finds haploid counts in *Oryzias* (*Haplocheilus*) varying from 22 to 24. The fact that fish are not favorable for cytological investigations is the most serious drawback for their use as material for genetic studies.

DEVELOPMENT

It has been suggested above that fish are likely to prove favorable material for studies bearing on the development of genetic characters. This is because the embryology of fish (especially the oviparous or spawning types) can be much more readily studied than that of other vertebrates. The egg is often transparent, the development is rapid and the embryo is not hidden by egg shell or enclosed within the body of the parent. The development is relatively simple and free from complications of metamorphosis such as are present in insects.

The embryonic and later history of the Mendelian characters described by Aida (1921) for *Aplocheilus* (*Oryzias*) *latipes* have been in part traced by Goodrich (1926, 1927). As the characters involved are color varieties the paper presents a study of the pigment cells or chromatophores. The phenotypic condition induced by the various genes is indicated by table 2. Herein it is indicated that in all phenotypes all pigment cells are present but the development of the pigment in these cells varies with the different types, though counts of chromatophores indicate that the same number of these cells is present in all cases. Hence it is apparent that the Mendelian character is not, in this case, produced by "energy of division" of cells (such as a greater multiplication of black chromatophores in the brown type) but rather by some other mechanism operating upon or within a constant number of cells. Observations on the young and embryonic stages confirm this concept. That this effect can not be due solely to an extracellular agent (such as a hormone) is shown by the conditions in the variegated type where some black chromatophores are heavily pigmented while in neighboring cells little pigment is developed. The conditions suggest that at an early stage there may be an embryonic segregation of anlage for deeply and for lightly pigmented cells and that they then migrate to form the color pattern of the variegated type. That the segregation must occur very early in development is indicated by the fact that Mendelian ratios may be obtained within two days after fertilization at about the stage of nine somites. Gordon (1927) in his analysis (see table 4) indicates clearly the cellular effect of different genes. The chromatophores primarily influenced by genes *Sp*, *St*, *R* are quite distinct. In the case of *Sp* and *St* there are two different

types of black chromatophores differing in size and in form. In goldfish it is possible that a quite different mechanism for color production prevails. Chen (1928) reports that in them there is a complete absence of yellow chromatophores and a great reduction of melanophores in the homozygous shubunkin, though Fukui (1927) reports that the varied colors of many goldfish are produced by the actual disintegration of pigment cells after a full complement was formed in the young stages.

Further complications are indicated by the phenomena of sex-reversal in fish as described by Blacher (1926), Winge (1927), and Essenburg (1923, 1926). In these cases there is clear indication that the action of hormones brings out the characteristic male color pattern. It seems to the writer highly improbable for reasons mentioned above in connection with the observations on the chromatophores in variegated *Oryzias*, that hormones alone can produce color pattern because their distribution is likely to be uniform through the blood stream, but a hormone acting on differing groups of cells might have such an effect. A complete understanding of these examples of coloration in fish would go far toward solving many problems of color pattern.

LIST OF LITERATURE

AIDA, TATUO. 1921. On the inheritance of color in a fresh water fish, Aplocheilus latipes, Temmick and Schlegel, with special reference to sex linked inheritance. Genetics, 6, No. 6, pp. 554–573.

APPELLÖF, A. 1894. Über einige Resultate der Kreuzbefruchtung bei Knochenfischen. Bergens Museums Aarbog for 1894–95.

BADE, E. 1898. Der rote Zahnkarpfen (Aplochilus latipes Blk). Bl. f. Aquar. u. Terrar. Fr., Jahrg. '98, pp. 240–241. 1 fig.

BANCROFT, F. W. 1912. Heredity of pigmentation in Fundulus hybrids. Jour. Exp. Zool., 12, pp. 153–178.

BELLAMY, A. W. 1922. Sex linked inheritance in the teleost Platypoecilus maculatus Günth. Anat. Rec., 24, pp. 419–420.

———. 1924. Bionomic studies on certain teleosts (Poeciliinae). I. Statement of problems, description of material and general notes on life histories and breeding behavior under laboratory conditions. Genetics, 9, pp. 513–529.

———. 1928. Bionomic studies on certain teleosts (Poeciliinae). II. Color pattern inheritance and sex in Platypoecilus maculatus (Günth). Genetics, Vol. 13, No. 3, pp. 226–232.

BLACHER, L. J. 1926a. Fall von Hermaphroditismus bei Lebistes. Trans. of the Lab. Exp. Bio. of the Zoopark of Moscow, Vol. 1, p. 95.

———. 1926b. Dependence of secondary sex-characters upon testicular hormones in Lebistes reticulatus. Bio. Bull., Vol. 50, No. 5, pp. 374–381.

———. 1927. Materials for the genetics of Lebistes reticulatus. Trans. Lab. Exp. Biol. Moscow, Vol. 3, pp. 139–152.

BLACHER, L. J. 1928. Material on the genetics of Lebistes reticulatus. Trans. Lab. Exp. Bio. Zoopark Moscow, Vol. 4, pp. 244–252.

BRÜNING, CHRISTIAN. 1916. Der "schwarze" Xiphophorus. Wochenschrift für Aquarien und Terrarienkunde, Bd. 13, No. 11, 14, Mar. 1916, pp. 117–120.

CHAMPY, CH. 1923. Observations sur les charactères sexuels chez les poissons (avec demonstration). C. R. Soc. Biol., 88, pp. 414–417.

CHEN, SHISAN C. 1925. Variation in external characters of goldfish, Carassius auratus. Contr. Bio. lab. Sci. Soc. China, May 1925.

———. 1927. Variation, Evolution und Vererbung beim Goldfisch, Carassius auratus. Blätter für Aquarien und Terrarienkunde, Jahrg. 38. pp. 401–404.

———. 1928. Transparences and mottling. A case of Mendelian inheritance in the goldfish, Carassius auratus. Genetics, Vol. 13, pp. 434–452.

CONSTANTINESCU, G. K. 1928. Kreuzungsversuche mit Rivulus urophtalmus. Zeit. Ind. Abst. u. Vererb., Bd. 47, p. 341.

COURRIER, ROBERT. 1922. Étude préliminaire du déterminisme des caractères sexuels secondaires chez les poissons. Arch. d. Anat., d'Histol. et d'Embryol., Tome 1, pp. 115–144. 4 pls.

DEAN, BASHFORD. 1912–23. A Bibliography of Fishes. American Museum of Natural History, New York. 3 vols.

DEMEREC, M. 1928. Possible explanation of

Winge's findings in Lebistes reticulatus. Am. Nat., Vol. 62, No. 678, pp. 90–94.

Embody, G. C. 1918. Artificial hybrids between pike and pickerel. Journ. Heredity, Vol. 9, pp. 253–256.

Essenberg, J. M. 1923. Sex differentiation in the viviparous teleost Xiphophorus helleri Heckel. Biol. Bull., 45, pp. 46–96.

———. 1926. Complete sex reversal in the viviparous teleost Xiphophorus helleri. Biol. Bull., Vol. 51, pp. 98–111.

Fearnow, E. C. 1915. Goldfish; their care in small aquaria and pounds. Report U. S. Comm. Fisheries (for 1914), pp. 445–458.

Fraser, A. C., and Gordon, M. 1928. Crossing over between *W* and *Z* chromosomes of the killifish, Platypoecilus. Science, Vol. 67, p. 470.

———. 1929. The genetics of Platypoecilus. II. The linkage of two sex-linked characters. Genetics, Vol. 14, No. 2. (In press.)

Fukui, Ken-ichi. 1927. On the color pattern produced by various agents in the goldfish. Folia Anatomica Japonica, Vol. 5, pp. 257–302. 9 pls.

Geiser, S. W. 1924. Sex ratios and spermatogenesis in the top-minnow, Gambusia Holbrooki Grd. Biol. Bull., Vol. 47, pp. 175–212. 3 pls.

Gerschler, M. W. 1914. Über alternative Vererbung bei Kreuzung von Cyprinodontiden-Gattungen. Zeit. Ind. Abst. Vererb., Bd. 12, pp. 73–96.

Goodrich, H. B. 1916. The germ cells in Ascaris incurva. Jour. Exp. Zool., Vol. 21, pp. 61–100.

———. 1926. The development of Mendelian characters in Aplocheilus latipes. Proc. Nat. Acad. Sci., Vol. 12, pp. 649–652.

———. 1927. A study of the development of Mendelian characters in Oryzias latipes. Jour. Exp. Zool., Vol. 49, No. 2, pp. 261–287. 3 pls.

Gordon, Myron. 1926a. Melanophores of Platypoecilus, the top-minnow of geneticists. Anat. Rec., Vol. 34, p. 138. Abstract No. 71.

———. 1926b. Variation in the tropical, viviparous killifish, Platypoecilus. Anat. Rec., Vol. 34, p. 166. Abstract No. 133.

———. 1926c. Tropical aquarium fish-culture in industry and scientific research. Am. Fish. Soc. Trans., Vol. 56, p. 1–11.

———. 1927. The genetics of a viviparous top-minnow, Platypoecilus; the inheritance of two kinds of melanophores. Genetics, Vol. 12, pp. 253–283.

Haffner, Karl. 1912. Eine Kreuzung zwischen Xiphophorus helleri var. Guntheri und Platypoecilus masculatus var. pulchra. Bl. f. Aq. u. Terr., Jahrg. 23, pp. 595–596.

———. 1913. Nochmals die Kreuzung zwischen Xiphophorus strigatus Regan (= Xiph. helleri var. Guntheri) male × Platypoecilus maculatus var. pulchra female. Bl. f. Aq. u. Terr., Jahrg. 24, pp. 533–535.

Hance, Robert T. 1924. Heredity in goldfish. A note on the inheritance of dove-tails and telescope eyes in goldfish. Journ. Heredity, Vol. 15, pp. 177–182. 5 figs.

Harms, J. W. 1926. Beobachtungen über Geschlechtsumwandlungen reifer Tiere and deren F_1 Generation. Zool. Anz., Bd. 67, pp. 67–79.

Hertwig, Günther und Paula. 1914. Kreuzungsversuche an Knochenfischen. Archiv für Mic. Anat., Bd. 84, Ab. 2, pp. 49–88.

Huxley, Julian S. 1920. Note on an alternating preponderance of males and females in fish and its possible significance. Jour. Genetics, Vol. 10, pp. 265–276.

Innes, William T. 1921. Goldfish varieties and tropical aquarium fishes. Innes & Sons, Phila. 274 p.

Ishikawa, Chiyomatsu. 1913. Dōbutsu-gaku Kogi (Lectures on Zoology). Vol. 1. p. 372.

Ishiwara, M. 1917. On the inheritance of body color in Oryzias latipes. Mitteilungen aus der medizinischen Fakultät der Kaiserlichen Universität Kyushu, Bd. 4, pp. 43–51.

Jordan, David Starr. 1923. A classification of fishes, including families and genera as far as known. Stanford Univ. Publ., Univ. series, Bio. sci., Vol. 3, No. 2. pp. 77–254.

Jordan, David Starr, and Snyder, John Otterbein. 1907. A review of the Poeciliidae or Killifishes of Japan. Proc. U. S. Nat. Mus., Vol. 31, pp. 287–290.

Kopeć, Stefan. 1917. Experiments of the dependence of the nuptial hue on the gonads in fish. Biologia generalis, Vol. 3, hft. 3, pp. 259–280. 1 pl.

Kosswig, Curt. 1928. Über Kreuzungen zwischen den Telostiern Xiphophorus helleri und Platypoecilus maculatus. II. Mitteilung. Zeitsch. f. ind. Abst. u. Vererb., Bd. 47, pp. 150–158.

Loeb, J. 1912. Heredity in heterogeneous hybrids. Jour. Morph., Vol. 23, pp. 1–26.

Meek, S. E. 1904. The fresh water fishes of Mexico north of the isthmus of Tehuantepec. Field Col. Mus. Zool. Series, 5, lxiii and 252.

MEINKEN, HERMANN. 1925. Kreuzungen. Bl. f. Aq. u. Terr., Jahrg. 9, 36, pp. 477–479.

MELLON, IDA M. 1927. Fishes in the Home. Dodd Mead & Co.

MOENKHAUS, W. J. 1904. The development of hybrids between Fundulus heteroclitus and Menidia notata with especial reference to the behavior of the maternal and paternal chromatin. Am. Jour. Anat., Vol. 3, pp. 29–66.

MORGAN, T. H. 1914. Heredity of embryonic characters. The Sci. Monthly, Vol. 18, pp. 5–17.

———. 1926. The Theory of the Gene. Yale Univ. Press. 343 p.

———. 1927. Experimental Embryology. Columbia Univ. Press. 766 p.

MORRIS, MARGARET. 1914. The behavior of the chromatin in hybrids between Fundulus and Ctenolabrus. Journ. Exp. Zool., Vol. 16, pp. 501–522.

NEWMAN, H. H. 1918. Hybrids between Fundulus and Mackerel. Jour. Exp. Zool., Vol. 26, pp. 391–422.

PETERS, W. C. H. 1859. Eine neue vom Herrn Jagor im atlantischen Meere gefangene Art der Gattung Leptocephalus, und über einige andere Fische des Zoologischen Museums. Monatsb. Akad. Berlin, 1859, p. 411–413.

PHILLIPPS, W. J. 1922. Hybridism of Salmo irideus and S. fario in Australasia. New Zealand Jour. Sci. & Tech., Vol. 5, pp. 98–100.

PINNEY, E. 1922. The initial block to normal development in cross fertilized eggs. Jour. Morph., Vol. 36, pp. 401–420.

———. 1928. Developmental factors in teleost hybrids. I. The early mitotic behavior in the cross between Menidia notata female and Rionotus carolinus male. Jour. Morph., Vol. 45, pp. 579–598. 2 pls.

REGAN, C. TATE. 1913. A revision of the cyprinodont fishes of the subfamily Poeciliinae. Proc. Zool. Soc. London, pp. 977–1018. 3 pls.

SCHMIDT, JOHS. 1919. Racial studies in fishes. II. Experimental investigations with Lebistes reticulatus (Peters) Regan. Jour. Gen., Vol. 8, pp. 147–153.

———. 1920. Racial Investigations. IV. The genetic behavior of a secondary sexual character. Comptes-Rendus des travaux du Lab. Carlsberg, Vol. 14, 1917–23, No. 8, pp. 1–12.

SCHREITMÜLLER, WILHELM. 1925. Danio albolineatus Blyth seine Pflege und Zucht und über einen Bastard von D. rerio H. G. × D. albolineatus Blyth. Bl. f. Aq. u. Terr., 36, No. 16, pp. 421–423.

———. 1926a. Über Xiphophorus helleri Heckel, seine Kreuzungsmöglichkeiten und Anderes. Bl. f. Aq. u. Terr., 37, No. 2, Jan. 1926, pp. 29–35.

———. 1926b. Ein Bastard von Brachydanio rerio H. B. (Zebrabarbe) × Danio malabaricus Jerdon. Bl. f. Aq. u. Terr., 37, pp. 440–441.

———. 1926c. Gambusia holbrooki, ihre Kreuzungsmöglichkeiten und Anderes. Bl. f. Aq. u. Terr., 37, No. 22, pp. 525–527.

TOYAMA, K. 1916. Itinino Mendel-seisitu ni tuite. (On some Mendelian characters.) Nippon Ikusyugakkukwai Hôkoku. (Report of Japanese breeding society), 1, pp. 1–9.

VAN OORDT, G. J. 1924. Die Veränderungen des Hodens während des Auftretens der sekundären Geschlechtsmerkmale bei Fischen. I. Gasterosteus pungitius L. Arch. f. Mik. Anat. u. Entw., Bd. 102, pp. 378–405.

———. 1925. The relation between the development of the secondary sex characters and the structure of the testis in the teleost Xiphophorus helleri Heckel. Brit. Jour. Exp. Biol., Vol. 3, No. 1, pp. 43–59.

WICHAND, B. 1906. Neuimportierte bezw. erstmalig nachgezüchtete Zahnkarpfen (Poeciliidae). Bl. f. Aq. u. Terr. Kunde, Jahrg. 17, pp. 495–496.

WINGE, O. 1922a. A peculiar mode of inheritance and its cytological explanation. Jour. Genetics, Vol. 12, pp. 137–144; also Comptes Rendus des Travaux du Lab. Carlsberg, Vol. 14, 1917–23, No. 17, pp. 1–10.

———. 1922b. One sided masculine and sex-linked inheritance in Lebistes reticulatus. Journ. Gen., 12, pp. 145–162; also Comptes Rendus des Travaux du Lab. Carlsberg, Vol. 14, 1917–1923, no. 18, pp. 1–20.

———. 1923. Crossing-over between the *X*- and the *Y*-chromosome in Lebistes. Jour. Gen., 13, pp. 201–217; also Comptes Rendus des Travaux du Lab. Carlsberg, Vol. 14, 1917–23, No. 20, pp. 1–18.

———. 1927. The location of eighteen genes in Lebistes reticulatus. Jour. Gen., 18, pp. 1–43.

THE CHEMICAL SENSES OF INSECTS

By DWIGHT ELMER MINNICH

Department of Zoology, University of Minnesota

JUST as the vertebrates are so frequently creatures of their visual and auditory senses, so the insects are largely creatures of their chemical senses. For it is chiefly by means of these senses that most insects find their food, their mates, and the food of their offspring, and that the social insects are enabled to make the manifold sensory discriminations necessitated by their highly complex social organization. It is not surprising, therefore, that this subject has received considerable attention. Indeed, in view of its importance, the surprising thing is that it has not received more attention.

The chemical senses of the vertebrates are separable into three clearly distinct categories, smell, taste, and the common chemical sense, each of which in turn appears to be capable of further resolution into a greater or lesser number of distinct senses (Parker, 1922). These categories are more or less closely related, and the distinctions between them have not always been clear. Thus, some of the earlier physiologists attempted to draw a distinction between smell and taste in the air breathing forms on the basis of the physical condition of the stimulus. For smell, the stimulus was thought normally to be a gas; for taste, a solution. Gradually, however, it became clear that in the case of the olfactory stimulus the gaseous particles, in order to reach the free ends of the sensory cells, must pass through the mucous solution in which these are enveloped. In other words, the gas must enter into solution. The situation is similar for the common chemical sense. In the vertebrate, therefore, the physical state of the adequate stimulus for all three groups of chemoreceptors is identical, viz., a solution of "chemically active material," in direct contact with the surface of the sensory cell (Parker, 1922, p. 168).

SMELL, TASTE, AND THE COMMON CHEMICAL SENSE

There are, nevertheless, certain characteristics by which these three categories of chemical sense may be differentiated. First, they differ with respect to anatomy and to distribution in the body. Second, they differ to a considerable extent with respect to the general classes of chemical materials which stimulate them. This is especially clear when smell and taste are compared. As Parker (1922, p. 170) remarks, "what is smelled is generally not tasted and what is tasted is not smelled." Third, they differ with respect to their threshold concentrations. This is well illustrated by the experiments of Parker and Stabler (1913) with ethyl alcohol, a substance which affects smell, taste, and the common chemical sense in man. The threshold for smell was found to be 24,000 times lower than that for taste, which in turn was 2 or 3 times lower than that for the common chemical sense.

Fourth, they differ with respect to the rôles played in the economy of the organism. Smell is usually concerned with directing the animal to a more or less distant source of stimulation,—food or a mate; taste, largely or solely with digestive reflexes, in the broad sense; the common chemical sense, with the detection of substances which are irritating and, hence, unfavorable to the animal's well being.

Whether the insect, like the vertebrate, possesses clearly distinct senses of smell and taste has been a matter of some discussion. Thus, McIndoo (1916, 1926) is of the opinion that in insects there is no true sense of taste and that apparent taste discriminations are to be attributed to a very highly developed sense of smell. This opinion is based on morphological work on the honey bee and the cotton boll weevil, in both of which he failed to find sense organs on the mouth parts which appeared to him suitable for organs of taste. The only sense organs found were various types of innervated hairs and the organs which have been named by him "olfactory pores." The first of these he believes to be anatomically unsuited to chemical stimulation. The second he finds to be identical in structure with the olfactory pores located elsewhere on the body, to which he attributes an olfactory function. As will be shown subsequently, however, recent work (Minnich, 1926b; v. Frisch, 1927) substantiates the viewpoint that there is quite as much ground for separating smell and taste in the insect as there is in the vertebrate.

Whether in addition to smell and taste the insect possesses something comparable to a common chemical sense, cannot be stated at present with certainty. Insects do respond to irritants, but the nature of the receptors concerned is not yet clear. The preliminary experiments of Hartwell (1924) may indicate a set of receptors for irritants, distinct from the olfactory receptors. Further experimentation must, however, determine this question.

WHERE ARE THE OLFACTORY ORGANS OF INSECTS LOCATED?

By far the greater part of the work on the olfactory sense of insects has been directly or indirectly concerned with the location of the sense organs and the determination of their structure. Many years ago Forel (1908, p. 74) opened a discussion of the olfactory sense in insects by saying that so much had been written on the subject that it was almost like gilding refined gold to return to it. Nevertheless, a great deal has been added to our knowledge of this subject since Forel wrote, and there is undoubtedly a very great deal yet to be learned.

During the eighteenth and the earlier part of the nineteenth centuries, the olfactory organs of insects were assigned by different writers to various locations, including the spiracles, the tracheae, and almost every conceivable location on the head and its appendages (cf. McIndoo, 1914c). Toward the end of the nineteenth century, however, through the work of Forel (1908), Hauser (1880), and others, the antennae came to be generally accepted as the seat of the olfactory sense. A summary of the evidence which led to this conclusion is given by Forel. In so far as the evidence was experimental it consisted in observing the responses of various insects to odors before and after antennal elimination, the antennae being eliminated either by amputation or by being covered with some presumably impervious material.

A rather striking experiment carried out by Mayer (1900) on the moth *Promethea* deserves especial mention in this con-

nection. Having shown experimentally that the males of this species are attracted to the females solely by chemical means, Mayer carried out various operations on the males. He found that males with the entire abdomen removed were still attracted to the female in normal fashion. If, however, the antennae of a male were covered with an impervious layer of photographic paste, it no longer sought the female nor displayed any excitement even when placed within an inch of her. In five such animals the paste was subsequently dissolved off with water, with the result that four of them "readily mated with the females." Upon again covering the antennae, however, "the males again failed to notice the females." Experiments of this sort certainly constitute very convincing evidence in favor of the antennae as seats of olfactory sense.

THE EXPERIMENTS OF VON FRISCH

Further evidence on this question has recently been afforded by the brilliant work of the German physiologist, v. Frisch (1921), on the honey bee. At a favorable spot out of doors, this investigator set up an experimental table on which was placed a row of four small cubical porcelain boxes, each provided with a circular entrance, 1.5 cm. in diameter, near the bottom of one face. Three of these boxes were empty and odorless. The fourth by virtue of a few drops of an oil placed inside was filled with a flowery odor, which emanated through the opening to the outside. This box also contained a dish of sugar water. By gradual steps, bees were trained to come to the table and to enter the odorous box in search of the sugar water. Each bee thus trained was marked on the thorax with a fleck of paint of a different color, by means of which careful records of the behavior of each individual could be kept. Frequent changes in the position of the odor box with respect to the others soon showed that the bees always went directly to the odor box. An association, quite independent of the position of the box, had thus been established between the odor and the presence of food.

After a few bees had been thoroughly trained, a period requiring about one hour, they were carefully caught, and the two antennae amputated. So skillfully was the whole procedure carried out that it apparently disturbed the bee very little, for immediately upon release she resumed her search for the odor box. While the operation was in progress, however, the four old boxes were replaced by four new ones, three of which were again odorless and empty, while the fourth carried the odor but lacked the sugar water. The odor box was also shifted to a new position in the row. The bees without antennae now hovered in front of first one box, then another, and entered the odorless boxes as frequently as, or more frequently than, the odor box.

In answer to the objection that the results might be due to the shock of operation rather than to the loss of specific sense organs, v. Frisch carried out an ingenious check experiment, using color instead of odor. The front of the box containing sugar water was covered with blue paper; the front of the empty boxes, with yellow paper. Removal of the antennae of animals trained to blue, however, failed to alter in the slightest degree the association with color. In every other respect, too, he reports that the behavior of the bees appeared to be normal. The ability to distinguish odor alone was gone. These results, together with the results of other more or less similar experiments, led v. Frisch to con-

clude that the olfactory organs must be located on the antennae.

In order to discover more exactly the location of the sense organs concerned, various experiments were carried out in which only portions of the antennae were removed. The results showed that so long as the fourth flagellar segment of one antenna remained intact, the bees could still distinguish an odor to which they had been trained or even be trained to a new odor. Indeed if only the proximal three-fourths of this segment remained there still persisted clear traces of olfactory discrimination for a time after the operation. With the complete elimination of this segment, however, olfactory discrimination disappeared.

THE PORE PLATES

Morphological study of the antenna with particular reference to this segment showed that the organs concerned were the so-called pore plates. The chitinous outer portion of these sense organs consists of a thick, oval plate surrounded by a narrow ring which is exceedingly thin. The sensory fibers terminate under the thin ring and not under the thick central portion, as previously thought. Hence the sense organs are structurally suited to the reception of chemical stimuli. The morphological as well as the experimental evidence thus indicates that the antennal pore plates of the honey bee are olfactory receptors. Von Frisch also considers the sense cones of the antennae to be olfactory in function. More recent morphological studies of the antennae of Hymenoptera in general (Vogel, 1923; Wacker, 1925) have borne out these conclusions and have shown that the antennal end organs of olfactory sense in this group include pore plates, cones, and hairs.

Working on the location of the olfactory organs in termites, Hartwell (1924) tried the effect of applying local anaesthetics to the surface of the antennae of these animals. Although her experiments were carried out on such a small number of individuals that they are little more than suggestive, they seem to indicate a loss of the olfactory sense after anaesthetization of the antennae.

Indirect evidence of the antennae as seats of olfaction has also been furnished by Liebermann (1925). In a comparative study of the antennae of the muscid flies this investigator was able to show a definite correlation between the number of sense organs on the antennae and the olfactory requirements of the insect. Thus, the antennae of flies that obtain their food from flowers, which are present in profusion throughout the breeding season and which are readily distinguished visually, were found on the average to have only 494 sense cones in pits and 1478 on the surface. The antennae of flies feeding on filth, carrion, and dung, substances which are more occasional and less widely distributed in nature and which are difficult or impossible to distinguish visually, had on the average 820 pit cones and 2764 surface cones, or nearly twice as many as the first group. Finally, the antennae of *Oestridae* or bot-flies, in which the connection between the insect and its food supply is even more tenuous, had 4683 pit cones and 1700 surface cones.

THE OLFACTORY PORES

The more recent investigators, however, have not been unanimous in their opinion as to the location of the olfactory sense organs. In a series of publications beginning in 1914, McIndoo (1914a, 1914b, 1914c, 1915, 1917, 1918, 1920a, 1920b, 1926) has attempted to show two things: first, that the antennae are not the seat of the olfactory organs; and second, that the latter are the structures called by him

"olfactory pores," which are located chiefly on the wing bases and the proximal portions of the legs, but also in small numbers on various other parts of the body.

In support of these contentions McIndoo offers the following arguments:

1. In the antennae the distal ends of the sensory terminals are covered with chitin, whereas in the olfactory pores they are exposed to the air. Hence, the latter are better suited to the reception of chemical stimuli than the former.

2. Any operation on the antennae renders the animal abnormal, so that failure to respond following this may be due to the general effect of the operation rather than to the elimination of olfactory organs. A measure of normality in behavior is post-operative longevity.

3. The reaction time (that is, the time required for a quiet animal to make any movement) to essential oils and other odorous substances is not significantly changed by eliminating the antennae, but it is greatly prolonged by eliminating the olfactory pores of the wing and leg bases.

To each of these arguments, serious objections may be offered. Concerning the actual penetration of the chitin by the sensory terminals of the olfactory pores, it may be said that most insect histologists believe that the outer chitinous layer is broken at no point. It may be exceedingly thin, as thin as half a micron over certain sensory terminals according to Snodgrass (1926), but it is always present. Furthermore, Eidmann (1922) has shown experimentally that chitin is not impervious at least to such substances as acids and alkalis. The evidence, therefore, seems to favor the view that all chemoreceptors are covered with at least a thin layer of chitin, through which the stimulating material must pass to reach the sensory terminals, rather than that the latter are exposed.

That any antennal operation renders the behavior of the animal so abnormal as to be unreliable, seems likewise not to be borne out by the facts. The work of v. Frisch (1921) on the honey bee, on which McIndoo did much of his work, certainly does not corroborate this. As v. Frisch points out, one may remove the eight distal segments of one antenna and the seven distal segments of the other, a total of fifteen segments, without the loss of such olfactory discrimination as his experiments demanded. But if the eight distal segments are removed from both antennae, a total of sixteen segments, olfactory discrimination is gone. The difference in the results following these two operations can scarcely be due to a difference in the extent of injury or shock. Nor is the idea that antennal elimination is always followed by marked abnormality of behavior, as indicated by short post-operative longevity, borne out by recent work. In some experiments with the cabbage butterfly, which I undertook a few years ago (Minnich, 1924), several individuals lived for about three weeks following antennal removal, and Abbott (1927a) has recently reported Necrophorus beetles still alive, six weeks after the same operation. In view of these facts, I do not believe that we are warranted in attributing the lack of response following antennal elimination to general abnormality of behavior.

The third argument mentioned is based on length of reaction time. According to McIndoo there is an inverse relation between the number of olfactory pores present and the average reaction time to odors. The following examples will illustrate the point for the honey bee. The odorous substances employed were oil of peppermint, oil of thyme, oil of wintergreen, honey, pollen, and leaves and bits of stems of pennyroyal. Drones were found to have 2600 olfactory pores, and an

average reaction time to these six odors of 2.9 seconds; workers, 2200 pores, and a reaction time of 3.4 seconds; queens, 1800 pores, and a reaction time of 4.9 seconds. Similar results were obtained when various groups of olfactory pores were eliminated by one means or another. Thus, in the worker the pores located on the wing bases constitute two thirds of all the pores present in the body, and their elimination increased the reaction time about eight times. In contrast to these results, it was found that the elimination of the antennae, which lack "olfactory pores," failed to alter the reaction time appreciably. From such results, McIndoo argued that the "olfactory pores" must be olfactory organs.

From a physiological viewpoint it is easy to understand how a difference in the number of sense organs might be correlated with a difference in the degree of responsiveness. In other words, the more sense organs the insect possessed the more vigorous its response to a given stimulus might be. But it is certainly difficult to see why differences in the number of sense organs present should be correlated with differences in the time of response. The point in question is illustrated by an observation made by Crozier (1915) on chemical stimulation of the skin of the frog. Crozier found that the time required for a spinal frog to withdraw its foot from a salt solution was essentially the same whether the entire foot or only one half the length of the digits was immersed.

OLFACTORY ORGANS NOT CONFINED TO THE ANTENNAE

McIndoo's evidence, therefore, fails to show conclusively either that the antennae are not the seats of the olfactory organs or that the olfactory pores are the olfactory organs. This does not mean that the so-called olfactory pores may not be olfactory in function. They may be, but the evidence available is not conclusive on the point. One fact is, however, clearly brought out by McIndoo's experiments, namely, that insects still respond to the odors of essential oils after the elimination of the antennae, or of the olfactory pores. Nearly fifty years ago Hauser (1880) noted that certain beetles and certain Hemiptera still responded to such odors as turpentine and carbolic acid, after amputation of the antennae. Recently Hartwell (1924) has shown for termites, and Abbott (1927a) for certain common beetles, that there is a persistence of response to essential oils after the antennal elimination. The beetles employed by Abbott still responded after the elimination of the antennae and of the olfactory pores on the wing and leg bases. In all of these cases the stimuli used may have acted as irritants, and may have affected the animal through other sense organs than the olfactory organs.

McIndoo's bees, however, also responded to honey and pollen after antennal elimination. Other instances have also been reported indicating the persistence of olfactory discrimination after the complete elimination of the antennae. Using the extension of the proboscis as an indication of olfactory stimulation, the writer carried out some experiments with the cabbage butterfly (Minnich, 1924). After twenty to thirty hours of total inanition, these insects were found to become regularly responsive to appropriate odors. If one antenna was amputated, the response decreased about 6 per cent. If the remaining antenna was amputated there was a further decrease of 46 per cent, or a total decrease of 52 per cent. Experiments in which the antennae were covered with vaseline or a paraffin-vaseline mixture gave similar results. The elimination of the antennae thus decreased the response but failed to abolish it.

The results obtained by Abbott (1927a) on carrion beetles are similar. Beetles without antennae located and dug up decaying meat or cloth soaked in skatol, buried in the sand of the box in which they were kept. One individual of *Necrophorus americanus*, which had neither antennae nor wings, and in which the leg bases were covered with shellac, invariably found the meat within a few hours. There can be little doubt, therefore, but that olfactory organs are present elsewhere than on the antennae. Just where these organs are located and what their structure may be, is not known. They may be organs on the mouth parts; they may be the olfactory pores of McIndoo; or they may be still more widely scattered sense organs. Abbott (1927 a, b) has recently expressed himself as favoring the last of these viewpoints, viz., a general distribution over the surface of the body. In any event, it is becoming increasingly clear that although olfactory organs are present on the antennae they are not confined to these appendages.

THE PHYSIOLOGY OF OLFACTION

There has been a great deal of scattered work on the attraction of insects by odorous substances, most of which has been directly inspired by economic problems. Without attempting to review this literature, several of the papers dealing with the broader physiological aspects of this problem may be mentioned briefly. Barrows (1907) worked on the chemical substances responsible for the attraction of *Drosophila melanogaster* to its food, viz., fermenting fruit. Of a number of substances tested, the flies responded significantly to five: amyl alcohol, ethyl alcohol, acetic acid, lactic acid, and ethyl acetate, all of which occur in fermenting fruit. Under the conditions of the experiment the optimum concentration of ethyl alcohol was 20 per cent, and of acetic acid, 5 per cent. A mixture of 2½ per cent alcohol and ⅝ per cent acetic acid, however, yielded a better response than either alone at the optimum concentration. Recently, Brown (1928) has shown that the odor of the yeast upon which the larvae of the flies feed also serves to attract the flies in addition to the "odors usually associated with that yeast."

A striking case of insect attraction by odor was reported by Howlett (1912) for fruit flies belonging to several species of the genus *Dacus*. It was first found that oil of citronella exercised a powerful attraction for the males of these flies, the reaction being entirely confined to this sex. Further experiments (Howlett, 1915) showed that the attraction was due to the presence of methyl-eugenol in the oil of citronella. Experiments were, therefore, carried out with 1) eugenol, 2) iso-eugenol, 3) methyl-eugenol, and 4) benzo-eugenol. The first and fourth attracted no flies. The second, iso-eugenol, attracted the males of *D. diversus* very strongly and the males of *D. ferrugineus* to a slight extent. The third, methyl-eugenol, attracted the males of *D. zonatus* very strongly, and the males of *D. ferrugineus* to a considerable extent. The significance of these odor responses, however, was not clear, for Howlett was unable to connect them with sex attraction or food smells in any satisfactory manner. I have been unable to locate any subsequent papers of this author on this subject.

The most important systematic study of the physiology of olfaction in insects is the work of v. Frisch (1919) on the honey bee. Only a few of the results of this extensive and important work can be summarized here. Using methods similar to those previously described for this author, v. Frisch tested a series of 47 ethereal oils, and found that bees pre-

viously trained to the odor of one of these oils, namely, an essence of orange, singled out this odor with great certainty from most of the others. Four of the odors, however, were confused to a very considerable extent with the essence of orange. These four oils were all extracted in the same manner as the essence of orange from other species of citrus fruits, and all had in common, oil of lemon and linalool. Furthermore, to the human olfactory organ, these four odors were found to be more nearly like the essence of orange than any of the other odors employed. Further experiments showed, however, that the four odors in question were not completely alike to the bee, but only similar. The two odors most nearly alike, which can be distinguished by man only after considerable practice, also required long training for the bee to discriminate. Von Frisch concluded, therefore, that in these respects, the sense of smell in the honey bee was no more delicate than that of man.

THE OLFACTORY THRESHOLD

In addition to experiments permitting a comparison of the olfactory powers of the bee and man qualitatively, experiments were performed which allowed a quantitative comparison. The threshold concentration to which bees could be trained was determined for three odors: paraffin oil scented with the odor of tuberoses, bromstyrene, and methylheptenone. It was found in each case to be essentially the same or at least of the same magnitude as the threshold in man. These results on the bee differ from those on certain other forms. The males of certain moths are attracted to the females almost if not entirely by odor, and experiments indicate extraordinary olfactory acuity on the part of the males in perceiving this odor. Riley (1894) reports a case in which a male of *Philosamia cynthia* found its way to a female over a distance of one and a half miles. Unfortunately the conditions of the experiment, such as wind direction, etc., are not recorded. The results of Fabre's (1879–1904) classic experiments with other moths indicate a similar development of the olfactory sense. A single female of *Bombyx quercus*, of which this veteran naturalist had not seen a single example in twenty years of collecting in his locality, attracted no less than sixty males.

When we consider the size of the scent producing gland in the body of the female moth, and the volume of air in which the volatile product of this gland is diluted, it seems almost incredible that there can be a material concentration strong enough to stimulate. It is little wonder, therefore, that some zoologists have been tempted to believe in a non-material form of emanation, such as waves. But the ability of such waves to pass through simple air-tight containers in which the females are enclosed, indicates that we are dealing with a chemical stimulus. Like the mammals, therefore, the insects differ greatly in their olfactory powers, and man and the dog find their counterparts in the bee and the moth.

The olfactory sense of these lepidopterous males is not only quantitatively, but also qualitatively acute. Both Mayer and Fabre report that other strong odors are ineffective in making the odor of the female less discernible or less attractive to the male. Experiments carried out by v. Frisch with odor mixtures showed that bees also had, to a considerable extent, the ability to detect a small amount of the training odor in an odor mixture. In this respect the bees were found to exceed the average man in olfactory discrimination, but whether their olfactory powers would also exceed

those of a man trained in olfactory discrimination, such as a perfume expert, is not certain.

Numerous experiments were carried out by v. Frisch with pairs of substances, similar in odor, with highly interesting results. In man two substances of different chemical composition may smell much alike, and two substances of similar chemical composition may smell differently. The same is true for bees. Each pair of substances tested, in which the two members, despite dissimilarity of chemical composition, smelled similar to man, appeared also to have a certain similarity for the bee. The significance of the results obtained with the bee is obvious, as v. Frisch points out, viz., that there is much more common to the physiological bases of smell in man and in the insect than would be expected from such differently organized sense organs.

THE SENSE OF TASTE

Until the last few years, the sense of taste in insects has received relatively little attention. The work of Will (1885) and of Forel (1908) constitute most of the older experimental work. Their experiments consisted in offering bees, wasps, and ants sugar or honey, and then substituting the same adulterated with various substances which are salt or bitter to the human tongue, or which are poisonous. The acceptance or refusal was then observed, and in this way certain facts were learned with respect to the gustatory powers of the insect.

More recently this problem has been attacked by more refined methods, which promise much more accurate and critical results. As I have shown (Minnich, 1921), it is possible to investigate many aspects of the chemical senses of insects by choosing species with extensible mouth-parts, and by using the extension of the proboscis as an indication of chemical stimulation. Suitable animals for this purpose are certain of the large flesh flies, such as various species of *Calliphora* and *Phormia*. These insects can be mounted individually with a bit of wax on a wire handle, and thus readily manipulated. If fed twice a day on a 1M saccharose solution they may be kept alive and vigorous for a period of several weeks or more. If the flies are kept in a condition of satiety with respect to water, the effect of various other solutions upon the proboscis extension may be observed. Thus, if a minute brush saturated with distilled water is gently applied to the oral sucker of such an animal, there is no response; but if a similar brush saturated with a 1M saccharose solution is applied, violent extensions of the proboscis result (Minnich, 1926b). Clearly the sense organs of the oral sucker are able to discriminate between pure water and an aqueous solution of saccharose. A study of responses to other substances is now under way in my laboratory.

Using these methods, it is also possible, with care, to stimulate certain of the hairs of the oral sucker individually. The margins of the aboral surface of the oral sucker are clothed with hairs, the outermost of which are long and curved. Under appropriate conditions, the application of 1M saccharose to a single one of these hairs may effect a proboscis extension, whereas the application of water will not. Hence these hairs are gustatory in function. Insofar as I am aware, this is the first case in which it has been possible to identify positively, by local stimulation, a chemoreceptor in an insect, the nearest approach to it being the work of v. Frisch in connection with the pore plates of the antennae.

THE THRESHOLD FOR TASTE

Recently v. Frisch (1927) has published some highly interesting results of experiments on the sense of taste in the honey bee. After training bees to feed on sugar water at an experimental table, he substituted various concentrations of different sugar solutions, or sugar solutions adulterated with other substances, and observed whether the bees accepted or rejected the substitute. Unfortunately, this method fails, as v. Frisch points out, to measure the real degree of sensitivity of the animal in many cases. Thus an animal may refuse to drink sugar water of a given concentration, and yet be able to distinguish it from water. For saccharose solution the threshold was between M/4 and M/8, or about eight times more concentrated than the human threshold. Check experiments showed that the perception of the sugar solution was not due to smell nor to such physical properties as viscosity and osmotic pressure. Hence it was tasted in the real sense of the word. A wide difference was found between the bee and man with respect to other substances which are sweet to the human taste. Thus while fructose tastes twice as sweet as glucose to us, it tastes less sweet to the bee. Lactose, moreover, appears to be completely tasteless to the bee. Other substances which are sweet to us, such as the sugars galactose, rhamnose, arabinose, the alcohols mannite, sorbite, and dulcite, and such substances as saccharin and dulcin, appear to be almost or wholly tasteless to the bee. In no case are they sweet.

To test the sensitivity to acids, various concentrations of hydrochloric and acetic acids were mixed with 1M saccharose, and the concentration noted which was sufficient to cause great hesitation in the acceptance of the solution. For hydrochloric acid this was *n*/80, the pH of the solution being 1.9; for acetic, *n*/5, the pH of the solution being 2.7. Just as in man, therefore, the acetic has a greater effect than would be expected on the basis of the hydrogen ion concentration alone.

Experiments with sodium chloride showed that a concentration of *n*/2 in 1M saccharose solution was refused by the great majority, while a concentration of *n*/8 was accepted by all. Suspecting that although *n*/8 was taken, it was still perceived, v. Frisch devised a very clever means of testing the matter. A known amount of solution was put out, and a careful record kept of the number of visits required for the bees to remove it. From these data the average crop load was computed. For 1M saccharose containing either *n*/8 or *n*/16 NaCl this was less than for pure 1M saccharose. For 1M saccharose containing *n*/32 NaCl, it was the same. Thus, although the bees accept 1M saccharose, adulterated with NaCl up to *n*/4 NaCl, they are able to distinguish the NaCl in dilutions as great as *n*/16. Experiments on the sensitivity of the human tongue to these mixtures showed that the threshold for NaCl under the same conditions was about the same in man as in the bees.

With the bitter substances, however, the threshold of the bee was found to be much higher than in man. A 1M saccharose solution containing M/2000 quinine hydrochloride, which is strongly bitter to us, was accepted by all bees, while a similar solution containing M/500 quinine, which is horribly bitter to us, was drunk by many. Indeed it was not until the quinine reached a concentration of M/300 that the mixture was generally refused. Thus, while exhibiting many points of similarity with the sense of taste in man, the sense of taste in the honey bee also shows some striking differences.

TARSAL ORGANS OF TASTE

But the sense of taste in insects is not confined to the mouthparts. As I have been able to show (Minnich, 1921, 1922a, 1922b, 1926a) for certain butterflies and flies, it is also present in the tarsi. Indeed, scattered observations seem to indicate that the tarsal organs of taste are of general occurrence among the arthropods. If a mourning cloak butterfly be observed as it approaches a bit of decaying apple, it may frequently be seen to extend its proboscis the moment one foot makes contact with the apple. That the organs concerned are gustatory and not olfactory may be demonstrated by a simple experiment. If, under appropriate conditions, a red admiral butterfly, *Pyrameis atalanta*, is placed in a holder which grasps the two wings and allows the feet to rest on a small platform of wire screen, and a needle bearing a small cotton swab soaked in apple juice is held 1 mm. from the ventral surface of any one of the tarsi, there is no response. The moment the swab is allowed to touch the tarsus, however, the proboscis is immediately extended.

In *Pyrameis*, studies were made of the effects of various dietary conditions, such as total inanition, water diet, and 1M saccharose diet, on the responsiveness to water, to 1M saccharose, to M/10 quinine hydrochloride, and to 2M NaCl. It was found that the response to water was capable of absolute control. With the administration of sufficient water, the response fell to zero, and remained there as long as water was given the animal in sufficient quantity. If the animal were subjected to total inanition, however, the response to water rose more or less gradually to 100 per cent, where it remained until water was administered, or until the animal died. The response to 1M saccharose, on the contrary, could not be controlled by feeding 1M saccharose. No matter how much of this solution was given the animal, it still responded regularly to it. The curves of response to NaCl and quinine varied with the time and with the animal from 0 per cent to 100 per cent. In general they followed neither the curve of water response, nor the curve of sugar response, nor the changing dietary conditions, nor each other. The curves of response to water, to 1M saccharose, to 2M NaCl, and to M/10 quinine hydrochloride were thus quite independent of each other. From these facts, it seems fair to conclude that these three solutions are distinguished from each other and from water by the tarsal organs of taste.

Experiments with varying dilutions of saccharose were also made during these different dietary periods to ascertain whether there was any variation in the threshold of the response. The results showed that there was such a variation. During periods of total inanition followed by periods of water diet, the threshold of response to saccharose gradually fell. With the initiation of a new period of saccharose diet, it rose abruptly to a level of not over M/10, where it remained approximately constant throughout the period. The interesting and surprising thing about these experiments was the extent to which the threshold fell during periods of prolonged inanition with respect to saccharose. It was found that saccharose concentrations of M/3200, M/6400, or even M/12,800, in some cases, could be distinguished from distilled water by the animals. The tarsal sensitivity of *Pyrameis* to saccharose may thus be at times as much as 256 times that of the human tongue.

As our knowledge of the chemical senses of insects has increased, a more accurate comparison has become possible with the

corresponding senses of the vertebrates, including man. One striking outcome of this comparison is the discovery of many rather fundamental similarities. Between the chemical senses of insects and man, however, there appears to be one outstanding difference, and that is the greater acuity of these senses in many insects. Whether increased knowledge will further verify this distinction cannot, of course, be predicted. But that insects should be capable of exceedingly fine discriminations of this nature is to be expected, inasmuch as they are a group of organisms in which the chemical senses have come to play the dominant rôle in general behavior.

This paper was presented in part at the 1927 meeting of The Entomological Society of America at the Symposium on the Physiology of Insects.

LIST OF LITERATURE

ABBOTT, C. E. 1917a. Experimental data on the olfactory sense of Coleoptera, with special reference to the Necrophori. Ann. Ent. Soc. America, 20: 207–216.

———. 1917b. Further observations on the olfactory powers of the Necrophori. Ann. Ent. Soc. America, 20: 550–553.

BARROWS, W. M. 1907. The reactions of the pomace fly, *Drosophila ampelophila* Loew, to odorous substances. Jour. Exp. Zool., 4: 515–537.

BROWN, F. W. 1918. Odors and insects. American Museum Novitates, No. 299, 9 pp.

CROZIER, W. J. 1915. Ionic antagonism in sensory stimulation. Amer. Jour. Physiol., 39: 297–302.

EIDMANN, H. 1922. Die Durchlässigkeit des Chitins bei osmotischen Vorgängen. Biol. Zentralbl., 42: 429–435.

FABRE, J. H. 1879–1904. Souvenirs entomologiques. 7 me série, nos. 23, 24, 25. 8 me édition. Paris.

FOREL, A. 1908. The Senses of Insects. Translated by Macleod Yearsley. London, XIV + 324 pp.

FRISCH, v., KARL. 1919. Über den Geruchsinn der Biene und seine blütenbiologische Bedeutung. Zool. Jahrb., Abt. f. allgem. Zool. u. Physiol., 37: 1–238.

———. 1921. Über den Sitz des Geruchsinnes bei Insecten. Zool. Jahrb., Abt. f. allgem. Zool. u. Physiol., 38: 449–516.

———. 1927. Versuche über den Geschmackssinn der Bienen. Die Naturwissenschaften, 15: 1–20.

HARTWELL, RHODA A. 1924. A study of the olfactory sense of termites. Ann. Ent. Soc. America, 17: 131–160.

HAUSER, G. 1880. Physiologische und histologische Untersuchungen über das Geruchsorgan der Insekten. Zeits. f. wiss. Zool., 34: 367–403.

HOWLETT, F. M. 1912. The effect of oil of Citronella on two species of *Dacus*. Trans. Ent. Soc. London, 1912: 412–418.

HOWLETT, F. M. 1915. Chemical reactions of fruit flies. Bull. Ent. Res., 6: 297–307.

LIEBERMANN, A. 1925. Correlation zwischen den antennalen Geruchsorganen und der Biologie der Musciden. Zeits. f. Morph. u. Ökol. d. Tiere, 5: 1–97.

MCINDOO, N. E. 1914a. The olfactory sense of the honey bee. Jour. Exp. Zool., 16: 265–346.

———. 1914b. The olfactory sense of Hymenoptera. Proc. Phila. Acad. Nat. Sci., 66: 294–341.

———. 1914c. The olfactory sense of insects. Smithsonian Misc. Coll., 63 (9): 1–63.

———. 1915. The olfactory sense of Coleoptera. Biol. Bull., 28: 407–460.

———. 1916. The sense organs on the mouthparts of the honey bee. Smithsonian Misc. Coll., 65 (14): 1–55.

———. 1917. The olfactory organs of Lepidoptera. Jour. Morph., 29: 33–54.

———. 1918. The olfactory organs of Diptera. Jour. Comp. Neur., 29: 457–484.

———. 1920a. The olfactory sense of Orthoptera. Jour. Comp. Neur., 31: 405–427.

———. 1920b. The senses of insects. Ann. Rep. Smithson. Inst., 1920: 461–483.

———. 1926. Senses of the cotton boll weevil—an attempt to explain how plants attract insects by smell. Jour. Ag. Research, 33: 1095–1141.

MAYER, A. G. 1900. On the mating instinct in moths. Ann. and Mag. Nat. Hist., Ser. 7, 5: 183–190.

MINNICH, D. E. 1921. An experimental study of the tarsal chemoreceptors of two nymphalid butterflies. Jour. Exp. Zool., 33: 173–203.

———. 1921a. The chemical sensitivity of the tarsi of the red admiral butterfly, *Pyrameis atalanta* Linn. Jour. Exp. Zool., 35: 57–81.

MINNICH, D. E. 1912b. A quantitative study of tarsal sensitivity to solutions of saccharose, in the red admiral butterfly, *Pyrameis atalanta* Linn. Jour.Exp. Zool., 36: 445–457.

———. 1924. The olfactory sense of the cabbage butterfly, *Pieris rapae* Linn., an experimental study. Jour. Exp. Zool., 39: 339–356.

———. 1926a. The chemical sensitivity of the tarsi of certain muscid flies. Biol. Bull., 51: 166–178.

———. 1926b. The organs of taste on the proboscis of the blowfly, *Phormia regina* Meigen. Anat. Record, 34: 126.

PARKER, G. H. 1922. Smell, Taste, and Allied Senses in the Vertebrates. Philadelphia. 192 pp.

PARKER, G. H., and STABLER, E. M. 1913. On certain distinctions between taste and smell. Amer. Jour. Physiol., 32: 230–240.

RILEY, C. V. 1894. The senses of insects. Insect Life, 7: 33–41.

SNODGRASS, R. E. 1926. The morphology of insect sense organs and the sensory nervous system. Smithsonian Misc. Coll., 77 (8): 1–80.

VOGEL, R. 1923. Zur Kenntnis des feineren Baues der Geruchsorgane der Wespen und Bienen. Zeits. f. wiss. Zool., 120: 281–324.

WACKER, F. 1915. Beiträge zur Kenntnis der antennalen Sinnesorgane der Hymenopteren. Zeits. Morph. u. Ökol. d. Tiere, 4: 739–812.

WILL, F. 1885. Das Geschmacksorgan der Insekten. Zeits. f. wiss. Zool., 41: 674–707.

DEATH FROM LOW TEMPERATURE AND RESISTANCE OF PLANTS TO COLD

By GUNNAR NILSSON-LEISSNER
Svalöf Plant Breeding Station, Svalöf, Sweden

IN THE last few decades, as is well known, the problems of death from cold and winter hardiness have attracted much attention in modern plant industry. This has especially been the case since the origin of new varieties by plant breeding and the introduction of new varieties from foreign countries got in full swing. It, therefore, seems appropriate that, when a review of all problems of this kind appeared, it should come from the hand of a plant breeder. Recently Doctor A. Åkerman of the Svalöf Plant Breeding Station in Sweden has published a detailed report of more than ten years work along this line and at the same time has given a thorough and critical review of all questions concerned (2). It is at present, no doubt, the best and most encyclopaedic treatise on the topic available. On the basis of this book I shall give below a short statement of the present day status of this field of the biological sciences.

THE MECHANISM OF CELL DEATH FROM COLD

The first question that presents itself when one is dealing with these topics, is of course: What are the causes of death from cold? Many workers have dealt with this matter and many are the conclusions that have been drawn. As yet it does not seem possible to form a definite conception of the immediate causes of death from cold, arising from too abundant ice formation in the cells. Besides the ice formation low temperature in itself is able to provoke injuries. Every organism has a fixed minimum temperature, below which it cannot live for long, and in some plants this minimum temperature is considerably higher than 0°C. (9). At certain temperatures even the speed with which the tissue thaws out may be of importance (1). If the temperature, however, is below that point where the cells freeze to death then, of course, the speed of thawing out is of no consequence. In plant tissues the ice appears at first in the intercellular spaces. With continued cooling, as a consequence of the low vapor pressure when ice is present, either water must be extracted from the cells or ice formation must occur in them (16). The latter case is only possible when the temperature has fallen below the freezing point of the cell content. If the cell content, however, is undercooled then its vapor pressure may be higher than that of the ice. In this case water again will move out through the cell walls to the ice crystals in the intercellular spaces. This desiccation by freezing temperatures can be detrimental and kill the tissue; it is, however, not only the loss of water in itself but also, among other things, its mechanically coagulating influence on the plasmic colloids that is of importance (8).

Two main groups of factors play an especially important part in determining the association between resistance to cold

and other physiologic conditions in the plant cell. These are (1) the possibility of undercooling, and (2) the water-retaining power of the cell content and the resistance to ice formation thus originated. An association between the possibilities of undercooling and the cell size has been demonstrated in that tissues with small cells will be more readily undercooled, whereas tissues with large cells will freeze suddenly on the slightest shaking at or below the freezing point (18). The resistance of the cell content to ice formation depends partly upon the osmotic properties of the constituents dissolved in the cell sap (6) or, eventually, in the protoplasm, and partly upon the capacity for swelling of the plasmic proteins and other colloids (10, 11). With falling temperature the latter seems to grow as a result of an increase of the quantity of certain comparatively simple organic substances, such as hexoses and pentosans (2, 12, 14, 15). Disregarding these relatively simple conditions, one must also take into account a whole complex of other factors and circumstances that influence the resistance of the cell or the tissue to cold, e.g. the specific organization of the protoplasm and its chemical composition.

It is of great importance that in different varieties of many plant species a certain correlation can be demonstrated between resistance to cold and other easily determinable factors, such as the osmotic value of the cell content at the point of incipient plasmolysis (2, 4, 6, 13), the percentage of reducing sugars (2, 12, 13), and coagulable nitrogenous constituents (12), and the quantity of dry matter (3, 5, 12, 17). So in some plant species it is possible to get an idea of the winter hardiness by investigating these factors. E.g. in wheat it is appropriate to analyse the quantity

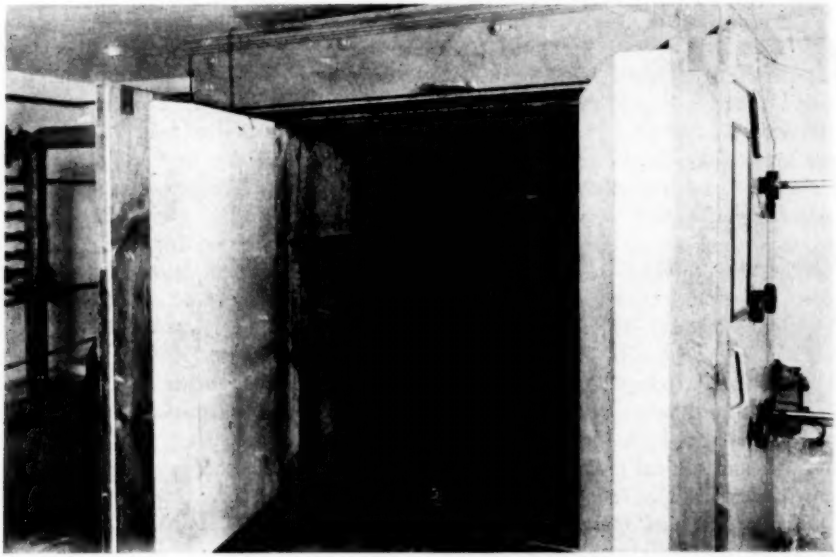


FIG. 1. THE REFRIGERATOR AT SVALÖF WHERE SMALL WHEAT PLANTS ARE EXPOSED TO LOW TEMPERATURE IN ORDER TO MEASURE THEIR RESISTANCE TO COLD

of dry matter, the osmotic pressure at incipient plasmolysis, the capacity of reducing Fehling's solution, and the resistance against expression of sap from the tissues by mechanical pressure (12). The direct refrigerator experiments might, however, be the most practical and reliable method for supplementing the working with crosses between rather hardy varieties, which one expects to be seriously injured by the winter cold only once in three or four years, it must be very valuable to be enabled by other means to select every year for winter hardiness. Such means are refrigerating experiments and investigations of the

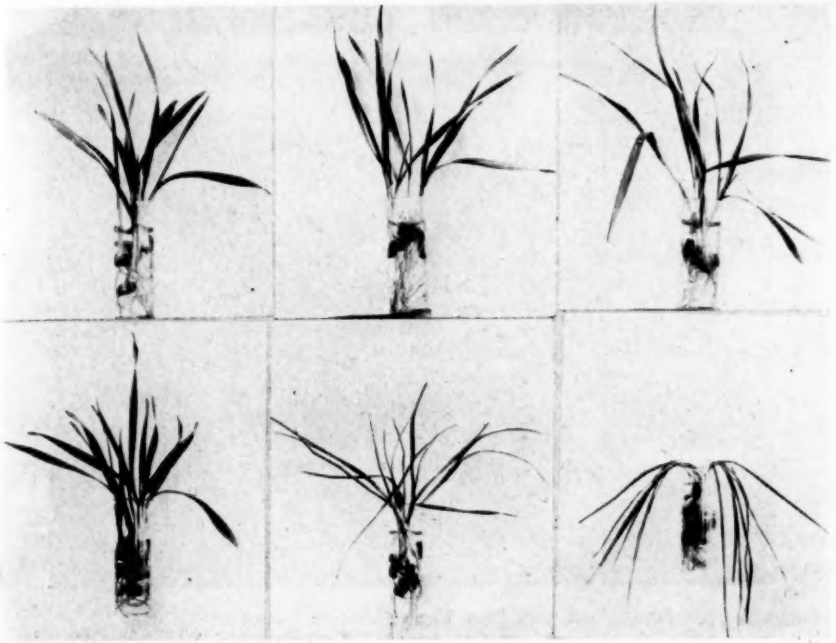


FIG. 2. PLANTS OF (FROM LEFT TO RIGHT) SWEDISH VELVET AND DANISH SMALL WINTER WHEAT AND HALLAND SPRING WHEAT; BEFORE (UPPER ROW) AND AFTER (LOWER ROW) 3 HOURS FREEZING TO −14.5°C.

observations in the field, whereas the other methods should be used more as a control and supplement to the first mentioned.

THE PREDICTION OF HARDINESS

As to the winter hardiness of different wheat varieties, it is evident that the possibility of its exact graduation in different ways must be of great importance to the plant breeder. For example, when above mentioned properties, correlated with cold resistance. The first thing to be considered must be what winter hardiness is and which different factors it depends upon. By a thorough and critical examination of the results of a great number of trials both at Svalöf and at the branch stations of the Swedish Seed Association, Åkerman (2) concludes that in Sweden resistance to cold is the most important factor determining the differences

of varieties in winter hardiness. Many other factors may partly account for winter hardiness, but towards these the investigated varieties all react in about the same way. Among such factors might be mentioned heaving, desiccation, damage caused by ice formation in the field, the vigor of the seed, and the stage of plant development depending upon it. The degree of winter hardiness of wheat might thus be well determined by means of refrigerator experiments. Åkerman has made a large number of such experiments by different methods in his refrigerator establishment at Svalöf designed for this purpose. It appeared that the most scrupulous selection and treatment of the plant material is needed for bringing out reliable differences as to resistance to cold of the individual varieties. The plants must all be of the same age and at the same stage of development. They must have grown under normal conditions in the field and must have been exposed to low temperature some time before they are refrigerated. Taking these precautions it is, however, possible by graduating the damage from cold of the frozen and again thawed out plants to get very close agreement as to the degree of winter hardiness with the results of the field trials and with practice. Åkerman has been able on the basis of the refrigerator experiments to classify his wheat variety material in ten different hardiness groups and in these groups he can also to a certain extent range the individual varieties. The order of varieties so obtained agrees strikingly well with many years observations of the field trials.

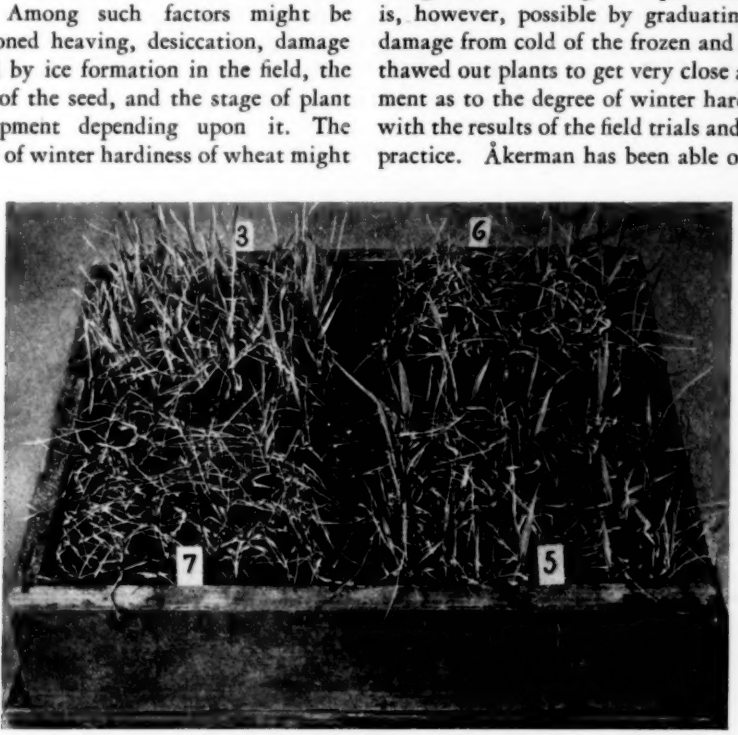


FIG. 3. FLAT WITH FOUR WHEAT VARIETIES FROZEN TO −12°C.
Nos. 3 and 5 hardly injured, most plants still living. No. 7 strongly injured, only a few plants living.

The determination of factors associated with resistance to cold has also been very successful. In co-operation with different chemists, particularly J. Lindberg, Åker-

man (2) has investigated the reducing capacity (sugar content) of leaves of individual cold resistant wheat varieties. In all varieties as yet examined an apparent correlation between reducing capacity and resistance to cold (winter hardiness) has been established, at least during the period of dormancy in winter. The samples should be taken at low temperature when the state of the weather is stable. In periods of highly variable weather changes in resistance to cold and sugar content appear that will give a conception of the variety differences quite different from the normal one. This is even the case in spring time when the plants start growing. Using three different methods: field trials, refrigerator experiments, and sugar analysis, good agreement between the different methods was obtained and, in the case of progenies from crosses, very reliable segregations as to low and as to high resistance to cold have been established. Even transgressive segregations could be shown in some cross progenies. As might be expected, the osmotic pressure of the cells in a state of incipient plasmolysis is closely associated with the reducing power (sugar content) of the wheat leaves and so can be used as a measure of resistance to cold.

LIST OF LITERATURE

(1) Åkerman, Å. Über die Bedeutung der Art des Auftauens für die Erhaltung gefrorener Pflanzen. Botaniska Notiser, 1919.

(2) ———. (In coöperation with Lindberg, J.). Studien über den Kältetod und die Kälteresistenz der Pflanzen nebst Untersuchungen über die Winterfestigkeit des Weizens. Publications of the Knut and Alice Wallenberg Foundation, X. Lund, 1927.

(3) Bakke, A. L., Radspinner, W. A., and Maney, J. T. A new factor in the determination of hardiness of the apple. Am. Soc. Hort. Sci. Proc., Vol. 17. 1920.

(4) Baroulina, E. I. On the resistance of winter-cereals to winter cold. Saratow, 1921.

(5) Beach, S. A., and Allen, F. W. Hardiness in the apple as correlated with structure and composition. Iowa Agr. Exp. Sta. Res. Bull. 21. 1915.

(6) Chandler, W. H. The killing of plant tissue by low temperature. Missouri Agr. Exp. Sta. Res. Bull. 8. 1913.

(7) Lidforss, B. Die wintergrüne Flora. Lunds Univ. Årsskr. N. F., Vol. 2, Section 3, No. 13. 1907.

(8) Maximow, N. A. Experimentelle und kritische Untersuchungen über das Gefrieren und Erfrieren der Pflanzen. Jahrb. f. wiss. Bot., Vol. 53. 1914.

(9) Molisch, H. Untersuchungen über das Erfrieren der Pflanzen. Jena, 1897.

(10) Newton, R. A comparative study of winter wheat varieties with special reference to winter-killing. Journ. of Agr. Sci., Vol. 12. 1922.

(11) ———. Colloidal properties of winter wheat plants in relation to frost resistance. Journ. of Agr. Sci., Vol. 14. 1924.

(12) ———. The nature and practical measurement of frost resistance in winter wheat. Univ. of Alberta Res. Bull. 1. 1924.

(13) Pantanelli, E. The resistance of plants to cold. Atti R. Accad. Lincei, Ser. 5, Vol. 27. 1918.

(14) Rosa, J. T. Nature of hardening in vegetable plants. Proc. Am. Soc. Hort. Sci., Vol. 16. 1919.

(15) ———. Pentosan content in relation to hardiness of vegetable plants. Ibid. 1920.

(16) Schander, R., and Schaffnit, E. Untersuchungen über das Auswintern des Getreides. Landw. Jahrb., Vol. 52. 1919.

(17) Strausbaugh, P. D. Dormancy and hardiness in the plum. Bot. Gaz., Vol. 71. 1921.

(18) Wibgand, K. M. Some studies regarding the biology of buds and twigs in winter. Bot. Gaz., Vol. 41. 1906.

NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

BRIEF NOTICES

EVOLUTION

ADDITIONS TO THE PALAEONTOLOGY OF THE PACIFIC COAST AND GREAT BASIN REGIONS OF NORTH AMERICA. *Contributions to Palaeontology from the Carnegie Institution of Washington. Publication 346.*
By Remington Kellogg, John C. Merriam, Chester Stock, Ralph W. Chaney, and H. L. Mason.
Carnegie Institution of Washington
$3.00 *Washington, D. C.*
6⅛ x 10; 158 (paper)

In this volume are included five studies:

I. *Study of the Skull of a Fossil Sperm-Whale from the Temblor Miocene of Southern California*, by Remington Kellogg. The author describes in great detail the fossil bones of an adult sperm whale and compares with this a partially preserved specimen of a young sperm whale of the same period and region. Nine plates give illustrations of both specimens.

II. *Fossil Pinnipeds from California*, by Remington Kellogg. In this paper are described the portions of the skull of a fossil pinniped, belonging to the group known as eared seals; also, portions of limb bones of two other species of fossil seals, probably of an undescribed form. There are eight figures illustrating the fragments described.

III. *A Hyaenarctid Bear from the Late Tertiary of the John Day Basin of Oregon*, by John C. Merriam and Chester Stock. This paper deals with several hyaenarctid teeth and fragments collected in 1925. The material proved to be some of the missing parts of a bear found in the same locality in 1925. Illustrations of the material are given.

IV. *Geology and Palaeontology of the Crooked River Basin, with Special Reference to the Bridge Creek Flora*, by Ralph W. Chaney. *With a chapter on the Tertiary Insects*, by T. D. A. Cockerell. The first part of this paper deals especially with a study of Tertiary floras of Eastern Oregon. Observations on the general geologic features made in connection with the work and a brief account of the vertebrate and invertebrate fossils found are included. The flora is extensively treated both quantitatively and qualitatively and local distributions are given. Twenty plates serve to illustrate the paper as well as to arouse in the reader a longing for the

opportunity to go hunting fossils in the Crooked River Basin.

V. *Fossil Records of Some West American Conifers*, by Herbert L. Mason. The fossil species of conifers are described in detail and the distribution of these, so far as known. A comparison is made with the present day distribution of conifers.

CREATION BY EVOLUTION. *A Consensus of Present-Day Knowledge as Set Forth by Leading Authorities in Non-Technical Language that All May Understand. Edited by Frances Mason.*

The Macmillan Co.

$5.00 5¾ x 8⅝; xx + 392 *New York*

A beautifully printed collection of essays by twenty-six English and American scientists, written, according to the Editor, "to render help to those who seek knowledge of the nature and bearings of the great fact of Evolution." There is a "Foreword" by Henry Fairfield Osborn, and an "Introduction" by Sir Charles Scott Sherrington. A group of selected references is appended to almost all of the articles. These in turn are usually followed by quotations from the writings of scientists or of otherwise famous men pertaining to the subject under discussion.

Each contributor discusses, in non-technical language, the meaning of evolution from the viewpoint of his own particular subject. It is at once apparent from a glance at the names of the distinguished men who have contributed that the book can justly claim authoritativeness of the highest order. Furthermore the writing is generally extremely well done, from a literary viewpoint.

For the professional biological reader, however, this book contains little that is new. For the general reader curious about the universe, it will furnish sound and interesting reading, much of which will certainly be novel. As for the fundamentalist, at whom this book was specifically aimed, we suspect, he can read these essays not only without having his faith in the Creator in any way shaken, but in the marvelous processes of Nature here disclosed he will be disposed to find a further and welcome confirmation of his belief in the far-sightedness and omnipotent skill of *Jahveh*. So it should, like Prohibition, leave everybody happy.

EVOLUTION AND WAR.

By Reginald Cock. *Elliot Stock*

3 s. 6 d. 4⅞ x 7½; 111 *London*

This is a new edition of the author's *Genesis v. Evolution*, reviewed here, along with his portrait, in March, 1927. The present work contains some scattered additions, and two new chapters, one on Civilization and one on War. The author is not one of the more formidable of Fundamental logicians, as the following sample will indicate:

> How comes it that Moses made no mistake? We can answer, only by inspiration; no human being witnessed creation, so an account of it, to be true, must be inspired by God. And it is reasonable to suppose that God Who gave man language, and the power to read and write, communicated to man those things which were necessary to his understanding and happiness.
>
> I quite agree with Sir Arthur Keith that it would be difficult for any modern teacher of medical students to assure his class, even in allegory, that the first woman was a modified rib. Following our Authorized Version we are in the habit of saying that Eve was one of Adam's ribs. But, as Lenormant says, the word *çêlâ* elsewhere means "side," and not rib.

We suppose that that makes it quite simple for a Christian.

WILD BIRDS INTRODUCED OR TRANSPLANTED IN NORTH AMERICA. *U. S. Department of Agriculture Technical Bulletin No. 61.*
By John C. Phillips.
Government Printing Office
10 cents *Washington, D. C.*
5⅞ x 9⅛; 63 (paper)

A list of the different species of birds whose introduction into North America has been tried, with accounts of the attempts. The material is of particular interest to the thoughtful student of evolution.

GENETICS

TWINS AND ORPHANS. *The Inheritance of Intelligence.*
By Alex. H. Wingfield.
J. M. Dent and Sons, Ltd.
10 s. 6 d. 5½ x 8; 127 *London*

This book, which is a thesis submitted in conformity with the requirements for the degree of Doctor of Philosophy in the University of Toronto, is an attempt to measure the relative importance of heredity and environment in determining general intelligence, intelligence being defined as the mental function measured by intelligence tests. The author's methods seem to us of somewhat dubious validity, especially in his treatment of his orphan population. He first states:

> If the cause, or partial cause, of the similarity found between twins or siblings is due to similarity of environment and training, we should expect to find that children who have been reared for a considerable period of their earlier lives, especially during the "plastic" period of early childhood, in a very nearly constant environment would show a fair degree of resemblance in various mental traits when paired with each other at random. In order to verify or disprove this hypothesis, the same tests that were given to the twins, as reported in the preceding portion of this study, were given to a group of orphan children who had been reared together for 25 to 75 per cent of their lives.

He then goes on to say: "Two methods of pairing the orphans were used. The first method was to pair an orphan with another who was nearest to him in chronological age. The second method was to pair the orphans with each other at random."

His findings as a result of this procedure are that "not only is there no resemblance when orphans are paired at random for intellectual traits, but there is a fair degree of inverse correlation. When the orphans are paired to the nearest age, we note in Table XXII that there is a slight degree of resemblance in the case of the I.Q.'s and arithmetic scores, while in the A.Q.'s and spelling scores there is a somewhat more marked correlation, although it is still low."

What we should like to know is what else he expected to get? If he took any population whatever, measured any character whatever, paired individuals at random, and determined the correlation coefficient, what value would he expect?

WILLIAM BATESON, F.R.S., NATURALIST. *His Essays and Addresses, together with a Short Account of his Life.*
By Beatrice Bateson. *The Macmillan Co.*
$8.40 5⅜ x 8¼; ix + 473 *New York*

This volume includes a memoir of Bateson by his wife, followed by a selection of his papers. The memoir is excellent reading, and gives a very attractive picture of Bateson's personality. It is somewhat lacking on the purely scientific side; we should like to see it supplemented by a fuller account of the development of Bateson's scientific ideas. Some of the papers will no doubt be familiar to professional geneticists; but they can be recommended generally. They include not only papers

specifically on heredity, but also papers on more general topics; in these we find much sound common sense, though we do find him saying that, "Prohibition, if it is maintained, will rank among the great disasters which from time to time have checked human progress." This, however, was written in 1919, and shows that he probably overlooked the ingenuity of Americans in developing adequate sources of supply to replace those cut off.

L'IMMUNITÉ DU NOURRISSON. *Contribution à l'Étude de l'Immunité Héréditaire.*
By Germaine Dreyfus-Sée. *Louis Arnette*
20 francs 6½ x 10; 194 (paper) *Paris*

The first part of this treatise is concerned with a review of what is known regarding congenital passive immunity, and its transmission from mother to child through the placenta, and through the milk. The second part deals with the tissue immunity of the baby. The author concludes that the infantile organism develops agglutinins very little if at all and has in general but feeble anti-microbic defense mechanism in the serum. It has, on the other hand, a remarkable resistance to toxic substances—drugs and the like. The third part of the book discusses true hereditary immunity, and contains an account of some interesting experiments with mice, in which two strains were bred differing widely in their resistance to pneumococcus infection. The book is a welcome addition to the literature regarding the genetic or constitutional factor in disease. There is an extensive bibliography.

VERHANDLUNGEN DES V. INTERNATIONALEN KONGRESSES FÜR VERERBUNGSWISSENSCHAFT BERLIN 1927. *Band I and II.*
Edited by Hans Nachtsheim.
Gebrüder Borntraeger
100 Marks for 2 volumes *Leipzig*
7½ x 10⅛; viii + 784 (paper)
viii + 785–1646 (paper)

These stately volumes contain the complete records of what was perhaps the most successful and important International Genetics Congress ever held. All the arrangements were extremely well managed. The volumes were promptly published and excellently edited. It is impossible to take the space here even to list the notable series of papers in all fields of genetics which were read at the Congress, and are here published in full. The Americans were well represented, both in respect of numbers and of the quality of the papers presented.

THE BOOK OF DOGS. *An Intimate Study of Mankind's Best Friend.*
By Ernest H. Baynes.
National Geographic Society
$2.00 6⅝ x 9⅝; 109 *Washington*

This volume describes and figures the principal breeds of dogs. It is beautifully illustrated. There are color portraits of 76 types from paintings by Louis Agassiz Fuertes and Hashime Murayama.

MUTATIONSTHEORIE DER GESCHWULST-ENTSTEHUNG. *Übergang von Körperzellen in Geschwulstzellen durch Gen-Änderung.*
By K. H. Bauer. *Julius Springer*
3.90 marks *Berlin*
5¾ x 8¾; 72 (paper)

A well-written and interesting little brochure developing the theory that

cancer arises as a somatic mutation, that is, a genic change in the chromosomes of a somatic cell. The author's main basis biologically is found in Boveri's classic memoir on the cytology of malignant cells, which by the way, is shortly to appear in English translation. Dr. Bauer is an associate professor of surgery at Göttingen and knows the clinical side well. Both medical men and biologists will find much that is suggestive in his theory.

HOW WE INHERIT.
By Edgar Altenburg.
Henry Holt and Company
$3.00 5⅜ x 8½; vii + 273 *New York*

A very readable little essay touching the principles of genetics sufficiently lightly to keep it unmarred for the reader who has "no previous knowledge of biology."

GENERAL BIOLOGY

PHYSIOLOGY AND BIOCHEMISTRY OF BACTERIA. *Vol. I—Growth Phases; Composition, and Biophysical Chemistry of Bacteria and their Environment; and Energetics.*
By R. E. Buchanan and Ellis I. Fulmer.
The Williams & Wilkins Co.
$7.50 6 x 9; xi + 516 *Baltimore*

This extensive work, only one volume of which is completed at present, has been planned with the view of placing in the hands of those especially interested in the subject, a compilation and systematization of material relating to the physiology of microörganisms, particularly of the bacteria, yeasts and molds. Much careful work has gone into the preparation of Volume I, which serves chiefly as an introduction and an outline of the subject. By this arrangement there is made apparent to the investigator many of the untouched fields of the physiology of microörganisms which are yet to be explored.

The book is well indexed, has 78 illustrations and a bibliography of several hundred titles. It will be particularly valuable to the general biologist. Bacteriology has become so specialized to particular ends that we all tend to forget that after all it is a branch of general biology. This treatise of Buchanan's and Fulmer's will serve well the extremely valuable purpose of making once more a closer *liaison* with the parent subject.

LA VIE, LA MALADIE ET LA MORT.
Phénomènes Colloidaux.
By Auguste Lumière. *Masson et Cie*
45 francs *Paris*
5⅛ x 8¼; xxiii + 520 (paper)

This volume is a continuation of the author's well known writings on the biological significance of colloids. It supports and further develops his thesis that the colloidal state is a necessary condition of life, and that the destruction of this state, that is to say the flocculation of the colloids, causes sickness and death. A short first part gives an elementary account of the properties of colloids. The second part, also short, discusses life in its relation to the properties and normal evolution of colloids, with particular reference to the phenomena of growth and senescence. The third and fourth parts, which make up the remaining two-thirds or more of this book, are concerned with pathological phenomena, especially in relation to the flocculation of colloids in the fluids and cells of the body. The book is well written and

illustrated. While its chief interest is special to the pathologist, the general biologist will find it worth reading.

THE CORAL REEF PROBLEM.
By William M. Davis.
American Geographical Society
$6.00 (to libraries $5.00) *New York*
6¾ x 10; 596

In this extensive research the author, who considers coral reefs, especially in their barrier and atoll forms, as among the most extraordinary of natural structures, has brought forth new evidence to support the theory of coral reef formation outlined many years ago by Darwin. He states that "as new facts have been brought to light, it has been most impressive to note the ease with which they have been explained by inevitable extensions of the old theory." He finds only one serious exception, namely the islands of the marginal belts of the coral seas. Here, "Darwin's theory must be supplemented by the wholly new process of low-level abrasion, first brought into the problem in recent years by Daly." Various other theories of coral reef formation are presented and discussed in detail.

There are numerous illustrations and diagrams throughout the text. A bibliography of several hundred titles and an excellent index complete the volume.

CILIARY MOVEMENT.
By J. Gray. *The Macmillan Co.*
$4.25 5⅜ x 8¾; viii + 162 *New York*

This volume is a study of ciliary movement from the physiological point of view. About half the book is devoted to a study of the mechanics of ciliary movements, including both the actual movement of the cilium itself and the work done by the cilium on the surrounding medium. There follow chapters on the relation of ciliary movement to ionic equilibria, on the metabolism of ciliated cells, on metachronal rhythm and ciliary control, with a final chapter on the distribution and functions of cilia in the animal kingdom. The book gives an excellent summary of our present knowledge, and a good indication of the directions in which further study is needed. There is a good bibliography and an index.

KAUSALITÄT UND VITALISMUS VOM STANDPUNKT DER DENKÖKONOMIE.
By Hans Winterstein. *Julius Springer*
4.80 RM. 6¼ x 9⅝; 51 (paper) *Berlin*

The second edition of an attack upon vitalistic philosophies and modes of thinking, by a distinguished experimental physiologist. He declares that his (and others') insistence on the necessity for physico-chemical explanations of the phenomena observed in living things is no dogma, as the vitalists insist it is, but is simply a necessary consequence and integral part of the very essence of explanation itself. We are unable to see that Winterstein contributes anything essential to this metaphysical discussion which has not already been said before, at least as well.

HUNTING UNDER THE MICROSCOPE.
By Sir Arthur E. Shipley.
The Macmillan Co.
$2.50 4¾ x 7½; 184 *New York*

This is a well-written little book, whose purpose is to encourage mucking about in ponds and ditches, and examination under the microscope of the results, by amateur

nature-lovers. It is very much the sort of book to give to a bright boy who has access to a microscope. We suspect that it would teach him vastly more than a good many school courses.

HUMAN BIOLOGY

HEALTH AND WEALTH. *A Survey of the Economics of World Health.* *By Louis I. Dublin.* *Harper and Brothers* $3.00 5½ x 8¼; xiv + 361 *New York*

The energetic statistician of the Metropolitan Life Insurance Company who is the author of this volume has earned the admiration of everyone interested in the advance of human biology. In exploring the records of his company for light on questions concerning broad biologic aspects of human pathology he has been a pioneer, and his recent writings with Lotka are fundamental for the theory of vital statistics. The present work is a collection of fifteen essays, selected from addresses, and is directed to the general reader. The topics are varied in character: the first three deal with the economic aspects of disease, the next three with heart disease, cancer and tuberculosis as they affect the general population, and the rest with various phases of vital statistics that are of immediate social interest, prohibition being one. All of them are clearly and interestingly written.

A zealousness on behalf of the public welfare runs through the work as its *Leitmotiv*. The author is everywhere ardent in advocating increased public activity for the sake of its own health. To no small degree this diminishes the objectivity of his studies, and lowers their critical scientific value. We would frankly apply this criticism throughout, but there is not space here for an elaborate analysis and the most we can do is to give several illustrations of our meaning.

On page 18 we read

> Where life is long, debilitating sickness is less prevalent and economic production is highest. The extraordinary prosperity which has been witnessed in the United States is, in large measure, the result of the control which has been exercised over disease; of the freedom which men and women have attained to labor without interruption and without fear; the opportunity that our children have gained to grow up in the care of father and mother, amply supplied with the necessities of life and preserved from the trials and sorrows of broken families. Where, as in India, the duration of life is short, existence is surrounded by fear of death, and of crippling, and of invalidism.

We submit that there is a possible confusion of cause and effect here.

In Chapter V, the author essays to determine the cause of the decline of the tuberculosis death rate. He sees two possible explanations, the first, that it is due directly to the deliberate modification of the environment by man.

> With that thought in mind, the proponents of this view early developed a broad campaign of general education of the population. A knowledge of personal hygiene was widely disseminated in order that individuals might learn how to strengthen their resistance against the development of active symptoms of the disease. This was the keynote of the general campaign against tuberculosis as outlined by this Association when it was founded in 1904.
>
> The campaign against tuberculosis was accordingly directed toward finding the large numbers of individuals who were breaking down with the disease, to strengthen their resistance, and to make them well again if possible, and, second, to prevent their infecting others.

The other minimizes the importance of environmental factors. "Those who support this second view emphasize the all importance of the genetic—that is, the constitutional factors." Pearl and Pearson are quoted as typical proponents of the second view. Now we do not speak authoritatively for either of the quoted

authors, but our impression is that their views and the issue are quite misstated here. The general question approached by them in different ways concerned a weighing of effectiveness as between the deliberate public health campaign against the disease, typified, for instance, in the above quotation from Dublin, and factors not associated with this direct attack. Inherited constitution is only one of these; others that come to mind as possible or even likely are decreased virulence of the bacillus, the gradual immunization of the community by small repeated infections, the improvement of physical condition incident to general betterment of economic status. Any considerable importance attached to such factors as these would as effectively weaken the case for large public expenditures for anti-tuberculosis campaigns as would the establishment of constitution as the significant determinant. But the author labors a long argument against the all sufficiency of the genetic explanation, and from his unfavorable result, makes the facile conclusion that the effectiveness of the public health attack on tuberculosis has been demonstrated.

Nor can we follow sympathetically, much as we admire the underlying work, the argument of Chapter IX on what the author calls the "true rate of natural increase." Here the point is made that the birth rate, and therefore any rate of increase derived from it, depends on the age distribution of the female population. The present population is artificially inflated, he says, in the child producing ages, a condition that will disappear as the population becomes stabilized. A rate of natural increase calculated for this stabilized population turns out to be 5½ instead of 11, which is the figure usually given. Now such a calculation assumes the constancy of existing age specific rates during the period required for stabilization. Lotka has estimated how long this should be, and if our memory is dependable it is something less than a century. For that length of time the death rates must remain stationary at their present value. Elsewhere, when the author is urging a different thesis, he estimates a 67 per cent decline of the tuberculosis rate in the next ten years! As a matter of fact the true rate of increase at any time is the quantity disparaged by the author, the existing death rate minus the birth rate; it is this figure that tells how many individuals are added to the population. To calculate for future decades what will be our rate of increase must include an estimate not only of what will be the future age distribution but also the future specific rates. Until such a calculation is made no such dire conclusion as the author's is justified.

After correcting for the purely incidental feature of a peculiar temporary age distribution, our natural rate of increase was reduced to one-half of its crude figure. We find ourselves, therefore, with a rather narrow margin of safety dividing us from the downhill slopes of actual population decrease.

HUMAN VALUES AND VERITIES.
By Henry Osborn Taylor.
The Macmillan Co.
$2.75 6 x 9; xiv + 282. *New York*

An elderly gentleman, a jurist, an historian, a philosopher who has a deep attachment to science, here sets down his thoughts on life's meaning. The devil's question—is it in its totality worth the living?—he circumspectly avoids, but out of his individual experiences he essays to synthesize a body of evaluating principles. "There ought to be some rational process, set in general human knowledge and experience, by which standards of worth

and truth suitable for thoughtful people might be established." Life's worth is found in two elements, values and validities. "What is of value to a man comes as an interwoven or organic response to a desire or activity of his own; in general, to his impulse to live and function. . . . . Indeed what is of human value seems identical with the very functioning itself of human faculty." Validity, which stands somewhat apart from value, has to do with the curiosity that impels man to objective truth. "Validity seems a realization within me of that which corresponds with fact, that is, with such reality as I may apprehend." The measure of these for the achievement of the good in life is to be found in their coördination in the whole being. "For the individual the final verdict upon the value of a given effort or the validity of a thought lies in the concert of his faculties—if such agreement can be found."

Provided with these criteria, the philosopher explores various departments of human faculty, history, science, philosophy, religion, practical affairs. In history, the author finds a changing of values and validities from age to age and from people to people. In the whole he sees progress. "I cannot survey the tale of history, with prehistory for prolegomena, without a conviction of human advance—only one must not think in decades or centuries, but in millenia or aeons." As between science and philosophy there is no real conflict; both are a response to thoughtfulness with a different psychological stress. "The philosopher is the thoughtful introvert, while the scientist is the rational observant extravert." And then again, in the chapter on Science proper, more grounds are found for a *rapprochement*. Philosophy is brought up to Spinoza and God, who "seems the infinite extended universe of being, law, and sequence, and has no purpose beyond itself." And so to the abiding religiosity of the writer.

In childhood, in boyhood intermittently, through youth and all the following years, I kept the habitude of prayer. It is still with me as a way of communion, a turning to the great Companion.

My life has been precious, wonderful, a thing to be grateful for to some Donor. I cannot think of myself as put together chemically or mechanically by "natural law." I must have a Cause that is all that I am.

Nothing here in this philosophical work to enlighten the epistomologist struggling to know what we know, nor yet to resolve the perplexities of the youth contemplating companionate marriage. Still, it is the authentic record of a mind that has achieved both knowledge and contentment.

THE STORY OF HAIR. *Its Purpose and Preservation.*
By Charles Nessler. *Boni and Liveright*
$2.50 5½ x 8; 277 *New York*

The author of this entertaining and instructive volume was formerly president of the American Master Hairdressers Association. Loquacious barbers are all too common; philosophical ones in the Johnsonian sense are occasionally to be found; but in hair-cutting, just as in every other line of human endeavor, a Newton or an Einstein only happens once in generations.

We shall let Mr. Nessler tell himself of his outlook and achievements.

When I, a boy of seventeen, following several years of youthful interest in the vagaries of human hair, went to work in a coiffeur's shop, the hairdressing profession had the status of an art or a trade—the designation in any instance depending upon the individual's skill. Today, after the passage of two decades, the treatment of human hair is in the process of becoming a science, a field of study that is full of

tremendous and hitherto unrealized possibilities, with social implications of far-reaching importance. To help it to this status, I have written this book, which represents many years of consistent research.

Between the day when I began to learn at first hand about the phenomena of human hair, and the time in which I have been writing this book, many things have happened in my chosen field of research. Indeed, many of these things I have helped to happen. The physical and mental sciences have been my aids, and the new viewpoints on the subject of human hair which I set forth here have been the result of the combination of scientific and psychological study.

In 1905, I brought forth my invention of the permanent wave, and when the late Professor Elie Metchnikoff witnessed a demonstration of it, he declared it to be the greatest advance ever made in hair science. Twenty years later came still another and vastly more important discovery, that of the classification of hair according to texture.

To achieve these forward steps, I personally observed, treated, and experimented with hair from thousands of heads. Simultaneously I had an opportunity to study the mental characteristics of those whose hair came under my notice, and to observe the relationship between the fundamental nature of the individual and the covering of his scalp. For years, in many countries and among many classes of people, I have sought the truth about human hair. I have been on terms of intimacy in every stratum of society. I have visited innumerable institutions—hospitals, orphanages, prisons, schools and factories, studying the relationship between the individuals I have found and the hair of their heads.

With the passage of years, observations became theories, and theories verified themselves until they became conclusions. My hair research left the field of science and entered the realm of psychology. In the last two decades there has been a tremendous advance in knowledge of psychological makeup of humankind. The behaviorists and the psychoanalysts have opened up new thought channels and new sources of understanding. To a world newly made aware of itself, I declare now that human hair is more than an adornment and appendage to mankind. It has serious meaning, and its importance to progress of the race cannot be underestimated.

What we like best in this modest recital of an obviously great accomplishment is the careful and precise distinction which Mr. Nessler repeatedly draws between psychology and science. What better guarantee could one have of his intelligence and insight?

The temptation to quote further from this book is great. We genuinely regret that lack of space forbids it, for we do like, when we can, to amuse as well as instruct the readers of THE QUARTERLY REVIEW OF BIOLOGY.

In closing this notice, however, we want to say, quite seriously, that this book is well worth reading by anyone interested in the study of human constitution. It contains, along with much nonsense, a great deal of probably sound information about human hair which is unknown to most biologists and medical men.

INFANCY AND HUMAN GROWTH.
By Arnold Gesell. *The Macmillan Co.*
$3.50 5⅝ x 8½; 418 *New York*

The author's purpose is to give an account of the development of human behavior and mentality during infancy. He presents a normative schedule of infant behavior at given ages, based on clinical observation of infants under controlled conditions. It is his thesis that the behavior of infants tends to develop uniformly, so that infants of a given age will show similar characteristic behavior in all items observed. On this point we find that the mothers with whom we have discussed the behavior of infants are not in agreement with the author: their statements are to the effect that normal infants vary greatly in the relative development of different behavior items, so that, for example, child A will talk long before he walks, while child B will walk long before he talks. Of course, such observations have small scientific importance when they are in opposition to

the conclusions reached in the psychological laboratory.

The author uses some very high-toned language; but he usually supplies a translation. For example, he says:

"The living eye can see but it cannot record. Not even in the visual arcana of the most eidetic cortex can permanent immutable images be stored for retrospective reference. This is just what the camera can do for us."

Again, he says:

"To some extent, then, the methodology of the observation of growth depends upon adjusting the durational interspaces between cross-sectional surveys of behavior levels in such a way as to yield a picture of the course of development."

This seems to say nothing more than that the intervals between observations should be of proper length; but it says it much more impressively.

THE CIRCLE AND THE CROSS. *A Study in Continuity. In two volumes. Vol. I.—The Circle.*
By A. Hadrian Allcroft.
Macmillan and Co.
12 s. 6 d. net *London*
$5\frac{3}{4}$ x $8\frac{3}{4}$; viii + 370

In this book the author gives the results of his studies on the derivation of the word church. It is a long path from the church yard of the Christians of the British Isles of the tenth century back to the mound moot of the Cymbrians of prehistoric times, but the author has traversed it with much skill and infinite pains and here presents in great detail his results. Because of this mass of detail the book will be of interest especially to the student of archaeology.

The author starts with the premise that the ground upon which stands a sacred building must be older than such a building. Therefore it is in the names given to such areas that he traces the origin of the word *church* although it is only in the final chapter that he arrives at a discussion of this word. The bulk of the book is taken up in tracing the circular church yards of the tenth century back to the mound barrows (burial places of the early Christians and pagans) and the sepulchral rings. These in turn he relates to the stone circles of the Cymbric Celts, which were used by them as moots, and finally to the older form of moots—the mound moots, or "hills of ceremony."

Having reached this goal the author proceeds to show how it is possible that the word church has come from the words *cruc* or *circ*, names, that the early peoples gave to the structures which were used for ritualistic or administrative purposes.

There are several plates and many text illustrations showing the various types of circles and mounds found in the British Isles.

THE DEAF-MUTE POPULATION OF THE UNITED STATES. 1910. *A Statistical Analysis of the Data Obtained at the Fourteenth Decennial Census.*
Bureau of the Census.
Government Printing Office
25 cents *Washington*
$5\frac{3}{4}$ x $9\frac{1}{8}$; 159 (paper)

The census enumerator has as part of his duties in collecting data for the decennial census that of obtaining certain records on all deaf mutes in the country. This volume is a statistical analysis of such data (1910 Census). Deaf mutes, as recorded, range from "those partially deaf, but able to hear only with ear trumpets or other mechanical devices" to "those literally unable to hear or speak."

The correspondence method was used in collecting the data.

Male deaf mutes, as in all previous censuses, are shown to be in excess of female deaf mutes. An analysis in age groups, however, shows that in childhood and youth there are more female deaf mutes than male; during early and middle adult life the males exceed the females; and in old age there is a return to an excess of female deaf mutes. The records giving an analysis of congenital deafness in the different races are interesting. The negro furnishes a larger proportion (56.4 per cent) of deaf mutes than any other race. Other plans of this study include marital conditions, education, methods of communication, economic conditions and causes of deafness. One hundred statistical tables are scattered throughout the text.

It is of interest to note that, according to the report, in those years (1880, 1890, and 1900) when the enumerator received five cents additional pay for each deaf mute reported on a supplemental schedule, the returns in deaf mutes were probably more complete than in the following years (1910–1920) when no additional pay was allowed.

FIRST REPORT OF THE PREHISTORIC SURVEY EXPEDITION. *The Oriental Institute of the University of Chicago Communication No. 3.*
By K. S. Sandford and W. J. Arkell.
University of Chicago Press
$1.00 7 x 9½; 52 (paper) *Chicago*

This report is intended to relieve the hypothetical layman who may be curious as to the *raison d'être* of a prehistoric survey in Egypt. The particular expedition dealt with here is part of the Prehistoric Survey of the Nile Valley and Western Asia organized by the Oriental Institute of the University of Chicago, and was to place special emphasis on the study of the geological record in Egypt. Most of the report is given over to an account of the prehistoric discoveries that have been made in Europe, and to an explanation of the blessings that would accrue to science if these could be correlated with findings on the African continent. The rest deals with the laborious journey of the two explorers southward from Cairo as far as Assuan, their return to Luxor by way of the east bank of the Nile, and their observations *en route*. At Koseir, on the coast of the Red Sea, human artifacts were discovered in this region outside the Nile Valley for the first time. There are a number of rather poor photographs, showing off mainly the vehicles of the expedition, a seven-horse-power Jowett and a Ford tourer, the Ford most of the time in trouble.

THE UNITED STATES OF AMERICA. *Studies in Physical, Regional, Industrial, and Human Geography.*
By Albert P. Brigham.
Oxford University Press
$3.00 5½ x 8⅝; x + 308 *New York*

This volume is the outgrowth of a course of lectures given at the University of London in 1920. Its motive is to give a general view of leading facts and principles of American geography. In the mind of the lay reader the word "geography" will probably arouse all of his early dislike of what has been in the past a dull subject. The introductory chapters over, however, there is much about the United States that is of general interest, especially in the sections on distribution of population, racial composition, growth of manufactures, the statehood complex, etc.

In the chapter devoted to traditions and language the author lays great emphasis on our debt to Great Britain and his belief that the deep sea of Anglo-Saxon tradition will absorb all that is alien to the principles and ideals which have been inherited from England through our Puritan ancestors. Was he trying to make out a case for his country before a British audience, or perhaps making a bid for an extra-special dinner in his honor, when he said: "Nothing is so fundamental to America as the demand for liberty, justice and order, in private and public life. The will to enjoy these blessings came with the founders from over the sea, and it has survived all the changes of circumstance, the pressure of environment and the mingling of new elements of population. The common law of England lies beneath us today."

VILFREDO PARETO. *Sa Vie et Son Oeuvre.*

By G. H. Bousquet. *Payot*

20 francs $5\frac{1}{2}$ x $8\frac{7}{8}$; 230 *Paris*

Vilfredo Pareto was, we believe, one of the very great men of our time. His work is little known as yet, but we have no doubt that knowledge and appreciation of it will spread for a long time to come. Beginning as an economist under the influence of Walras, he brought the mathematical theory of economic equilibrium to something like a final form. From economics he moved into sociology, impelled, one imagines, by the impossibility of describing human behavior purely in economic terms. His sociological writings aim at interpreting the behavior of men as social beings largely in terms of the fundamental non-logical motives which drive them.

His work is the most impersonal and detached with which we are acquainted; we doubt that anyone can find, in the *Sociologie Générale*, evidence on which to determine Pareto's opinion as to any of the questions about which men fight. He is nearer to the purely scientific observer than any other writer we know of.

The present volume contains a brief account of Pareto's life, and a summary of his work. It has considerable value as an introduction to Pareto's work, because of that distinguished author's carelessness with regard to literary form. There is a bibliography of Pareto's writings.

DIE RASSE IN DEN GEISTESWISSENSCHAFTEN. *Studien zur Geschichte des Rassengedankens.*

By Ludwig Schemann. *J. F. Lehmanns*

18 Marks (paper) *München*

20 Marks (cloth)

6 x $8\frac{3}{4}$; xvi + 480

A dull and pedantic treatise, with 1195 footnotes. It constitutes the first of three volumes to be devoted to a general evaluation of race and races. The point of view is essentially that which was much more entertainingly expounded some years ago by a Frenchman named Gobineau. The author points out that since Gobineau no one has gone quite so surely and keenly to the root of the problem of races as have Madison Grant and Lothrop Stoddard. The book concludes on a high note: "*Wir sagten es zuvor: 'Die Germanen oder die Nacht' ist heute die Lösung wie einst. Der Beruf der Germanen kann nie und nimmermehr erlöschen, er wird—wenigstens in der Idee—fortbestehen bis ans Ende der Tage.*"

We break a usual editorial rule and let this stay in its original language. It sounds better. And what a comfort it is to know that ours is not the only land

in which that pestilential microbe the One Hundred Percenter is endemic!

AGRICULTURAL SURVEY OF EUROPE: FRANCE. *United States Department of Agriculture, Technical Bulletin No. 37. By Louis G. Michael.*

Government Printing Office
25 cents *Washington*
5¾ x 9¼; 184 (paper)

The purpose and scope of these surveys are indicated as follows:

"The bulletins of the agricultural surveys of foreign countries will contain an analysis of the agricultural situation in each country from the viewpoint of the potential demand for agricultural products by those countries whose production is not sufficient to meet their national requirements and the nature and extent of the competition from foreign producers that the farmers of America must meet in disposing of their surplus in foreign markets. These surveys include a comparison between the prewar and postwar trends in the agriculture of the countries as affected by the economic conditions, territorial changes, if any, and other factors in each country, brought about by the World War."

THE LIFE OF A SOUTH AFRICAN TRIBE. *Vol. I. Social Life. Vol. II. Mental Life.*

By Henri A. Junod. *Macmillan and Co.*
50 shillings net *London*
5½ x 8½; Vol. I, 559
Vol. II, 660

These two volumes, a revised and enlarged edition of an earlier work, are by a member of the Swiss Romande Mission, who has lived many years among the northern clans of the Thongas of the Transvaal, and who has recorded for this particular tribe all that it was possible to learn concerning their manners and customs, their agricultural and industrial life, their art, religion and literature.

Although a missionary, the author has held himself strictly to the problem of placing on record all the information that he has been able to glean about the highly complex life of this group. Only at the very end of each volume under the heading of "Practical Conclusions" has he permitted himself to enter into a brief discussion of the various phases of their lives and the effect which the missionary and the white man has upon their *mores*.

Anthropologists will appreciate this new edition of a painstaking work, and the general reader who enjoys delving into books dealing with primitive peoples will find these two volumes highly interesting.

MY PEOPLE THE SIOUX.
By Luther Standing Bear.

Houghton Mifflin Co.
$4.00 5½ x 8; xiv + 288 *Boston*

This autobiography of a Sioux chief contains a certain amount of information relative to Indian manners and customs, but its main interest is as it illuminates the relation between the Indian and the white man. As set down by Standing Bear the asininity of the whites is appalling—especially in their efforts to be kind to the red men. His account of the early days of the Carlisle Indian School (he was one of the first pupils) is vastly entertaining.

It is to be hoped that some day the legend that Sitting Bull was responsible

for the Little Bighorn massacre will be put down, but the hope is slim. Standing Bear does his best to give Crazy Horse the credit that belongs to him; he unaccountably omits mention of Gall.

OBSERVATIONS ON HAWAIIAN SOMATOLOGY. *Memoirs of the Bernice P. Bishop Museum Vol. IX, No. 4. Bayard Dominick Expedition Publication No. 13. By Louis R. Sullivan (Prepared for publication by Clark Wissler).*

Bernice P. Bishop Museum
$2.00 *Honolulu*

9½ x 12½; 76 + 5 plates (paper)

In this publication are given the compilations of data which were made by Dr. Louis R. Sullivan on living Hawaiians with the object of determining the "elements entering into this stock and in turn to suggest the position of Polynesians with respect to other races." Owing to Dr. Sullivan's death Dr. Clark Wissler prepared the material for publication, in order that it would be in such shape that future students of the Polynesians could make use of it. The tables, of which there are 57, consist of anthropometric measurements and data on qualitative characters. Since Dr. Sullivan left no usable notes Dr. Wissler has commented briefly on the results which the data show. The original individual records and a key to them are included in the publication. This work will be of great value to anthropologists who are especially interested in the Pacific Races.

AN ANTHROPOMETRIC STUDY OF HAWAIIANS OF PURE AND MIXED BLOOD. *Papers of the Peabody Museum of American Archaeology and Ethnology, Harvard University Vol. XI, No. 3.*
By Leslie C. Dunn. Based upon data collected by Alfred M. Tozzer.

Peabody Museum
$1.75 *Cambridge, Mass.*

6¼ x 9½; 122 (paper)

There is in progress in Hawaii an extensive crossing of races, which offers obvious opportunities to the student of human genetics. In particular, extensive crossing is taking place between Hawaiian and Chinese, both of whom are probably relatively pure bred races, as human races go. The present anthropometric measurements are upon pure bred Hawaiians and upon crosses between native Hawaiians and other races. The numbers involved, when classified by sex, age, and race, form rather small series. The F_1 generation of Chinese ♂ × Hawaiian ♀, for example, contains only seven males and eleven females, which is, of course, wholly insufficient to warrant many conclusions.

The raw data from which the frequency distributions have been formed are given in an appendix.

JAWS AND TEETH OF ANCIENT HAWAIIANS. *Memoirs of the Bernice P. Bishop Museum Vol. IX, No. 3.*
By H. G. Chappel.

Bernice P. Bishop Museum
$2.00 *Honolulu*

9½ x 12½; 20 + 4 plates (paper)

Crania in the Bernice T. Bishop Museum, in Honolulu, most of which were of the period preceding the coming of white men, furnish the material for this study of the teeth and dental diseases of ancient Hawaiians. Well formed teeth with excellent enamel were characteristic of these specimens. Traces of evolutionary change,

variations in the two sexes, variability in the position of the mental foramen and irregularities in the cervical border of enamel are some of the topics treated statistically. A series of photographs exhibits the irregularities and diseases of the teeth. The work also included individual records of the mandibles and maxillae for both sexes.

AN EXPERIMENTAL STUDY OF THE EAST KENTUCKY MOUNTAINEERS. *A Study in Heredity and Environment. From the Psychological Laboratories of Harvard University and Duke University. Genetic Psychology Monographs Vol. III, No. 3.*
By Nathaniel D. Mttron Hirsch.
Clark University Press
$2.00 *Worcester, Mass.*
6⅝ x 9¼; 56 (paper)

This interesting study of the East Kentucky Mountaineers has as its primary problem to discover the causes and conditions of the generally low mental status, as exhibited by intelligence tests, of the inhabitants of a region which was originally settled largely by people of Scotch-Irish descent. Other problems closely associated with the main theme, which the author considers, are pigmentation and cephalic index, migration, the degree of consanguineous marriages, size of family, etc. A number of tables give the results of intelligence tests and anthropological measurements.

FOLKLORE OF THE TEETH.
By Leo Kanner. *The Macmillan Co.*
$4.00 *New York*
5 ½ x 8 ½; xiii + 316

A collection of superstitions, charms, legends, and popular pathology and medicine relating to the teeth. We regret that in referring to legends of individuals furnished with double and triple rows of teeth, there is no mention of Paul Bunyan's logger, Double Jawed Murphy, who chawed up the grindstone in his sleep. His account of St. Appolonia, the patroness of toothache, is entertaining, but he displays a lamentable scepticism in doubting the authenticity of her relics, merely on the ground that more than thirty-two of her teeth are on display.

THE BUILDING OF CULTURES.
By Roland B. Dixon.
Charles Scribner's Sons
$4.00 6 x 9; x + 312 *New York*

This book deals with the origin and diffusion of human culture. It is well written, and gives a balanced discussion of the fundamental problems involved. Its outlook is primarily theoretical, but the practical applications of theory to concrete problems are not neglected.

The author is strongly opposed to the more extreme forms of the diffusion theory, and his criticism of such theories as those of Elliot Smith is severe; he seems to us, however, to make good his case. The book may be recommended to anyone interested in anthropology, whether a specialist or not.

HUMAN MERCHANDISE. *A Study of the International Traffic in Women.*
By H. Wilson Harris. *Ernest Benn, Ltd.*
6 shillings net *London*
4 ¾ x 7 ½; 272

Mr. Harris has condensed and rewritten for popular consumption the two volume Report on the Traffic in Women and Chil-

dren published by the League of Nations in 1927. The original report is a valuable source document for the student of human biology. This little "re-write" has only ephemeral value and not a great deal of that. England, the United States and Switzerland make the best showing relative both to domestic prostitution and to export and import traffic in women.

MORTALITY AND THE DRY LAW.
By Deets Pickett.
Research Department of the Board of Temperance, Prohibition and Public Morals of the Methodist Episcopal Church
$1.00 *Washington*
7 ¾ x 10 ⅜; 97 (paper)

A piece of brazen propaganda wearing a thin guise of objectivity. The data comprise mortality statistics under various categories from 1910 to 1926, organized for the ostensible purpose of revealing any relation between them and the operations of the prohibition law. All the results point to the healthy effect of the statute on mortality. The fallaciousness of some of the conclusions is obvious, of others more obscure. None would be accepted, on the evidence given, by a statistician endowed in the slightest degree with critical sense.

LA PÊCHE DANS LA PRÉHISTOIRE DANS L'ANTIQUITÉ ET CHEZ LES PEUPLES PRIMITIFS.
By A. Gruvel.
Société d'Éditions, Géographiques, Maritimes et Coloniales
40 francs *Paris*
6 ½ x 10; 232 (paper)

A discussion of fishing, as carried on in prehistoric times, in ancient history, and among modern primitive races. The author points out the importance of fish as a source of food among primitive races, and urges that the colonial administrators take measures to encourage its production and distribution. The book is abundantly illustrated.

ZOOLOGY

NATURE AND EXTENT OF FOULING OF SHIPS' BOTTOMS. *From Bulletin of the Bureau of Fisheries, Vol. XLIII, 1927, Part II. Document No. 1031.*
By J. Paul Visscher.
Government Printing Office
35 cents *Washington*
7 ½ x 11; 60 (paper)

A report of an investigation of the nature of fouling of ships' bottoms, and the conditions determining its extent. Some of the conclusions reached are:

Fouling organisms are almost exclusively those commonly found on rocks and other submerged structures near shore, especially in harbors.

Fouling occurs almost entirely while vessels are in port.

Fresh water kills most of the organisms that cause fouling within 72 hours, but if calcareous or chitinous growths already have been formed, such materials remain and the resistance is not materially lessened.

Certain species of barnacles grew at a very rapid rate, attaining a size of 2 inches and becoming sexually mature within 60 days.

Certain barnacles are found attached on certain substances and in limited regions, indicating a relation between attachment and the nature of the surface.

Light has been found to be an important factor governing the attachment of the larvae of the forms that cause fouling.

At the time of attachment the larvae of *Balanus improvisus* and *B. amphitrite* are negative to light. (Most of the forms found on ships' bottoms probably are of a similar nature.)

Light in the field of green and blue has been

demonstrated to have the maximum stimulating efficiency for the cyprid larvae of several barnacles.

This report indicates the value of an intensive study of seasonal periodicity of fouling organisms, of the relation between fouling organisms at the time of attachment and surface films, and a study of properly prepared paints of lighter colors than those now in general use.

KEY-CATALOGUE OF INSECTS OF IMPORTANCE IN PUBLIC HEALTH. *United States Public Health Service Hygienic Laboratory Bulletin No. 150.*

By C. W. Stiles and Albert Hassall.

Government Printing Office

20 cents *Washington*

5 ¾ x 9; iv + 118 (paper)

A condensed, systematized compilation of the data of entomology as it applies to public health. It represents part 4 of Stiles and Hassal's Host Catalogue, Index Catalogue of Medical and Veterinary Zoology, prepared in special form for use at the Hygiene Laboratory. About a thousand entries alphabetically arranged are given and cross indexed with brief notes under the following headings:

A, biting insects; B, on cadavers or in graves; C, control of public-health pests; D, dermatology (lesions, dermatitis, eruptions, exanthema, parasites, urticaria); E, edible (food, drink); F, excreta; G, food and drink; H, jurisprudence; I, laity (fear, superstition); J, parasites and pseudoparasites (abdomen, ear, external, eye, head, intestine, miscellaneous, mouth, nose, stomach, subcutaneous, throat, and urinary system); K, pests (books, clothes, drugs, records, miscellaneous); L, pinching insects; M, poisons (arrows, defensive, food, spines, miscellaneous); N, pollution (air, water); O, stinging insects; P, therapeutics (lay, professional); Q, vectors (Aspergillus, bacteria, filth, Protozoa, Trematoda, Cestoda, Nematoda, Acanthocephala, Insecta).

THE SCORPIONS OF THE WESTERN PART OF THE UNITED STATES, *with Notes on those Occurring in Northern Mexico.* *By H. E. Ewing.*

Government Printing Office

Washington, D. C.

6 x 9½; 24 (paper)

An increasing demand for information concerning the scorpions of the south-west region of the United States has led the Bureau of Entomology to undertake a study of these venomous arachnids. In this, the first bulletin issued on the subject, a taxonomic synopsis is given of all the species reported for the United States west of the Mississippi, an account of what is known of the distribution, life histories and habits of the more common species, and also of what is known of the effects of the venom. Notes are included concerning species occurring in northern Mexico.

Since no extended work on scorpions has been issued within the last twenty years, the plan of the author to make a comprehensive study of them will be welcomed not only by entomologists, but also by the inhabitants of the region and travellers in it.

LEAF-MINING INSECTS.

By James G. Needham, Stuart W. Frost and Beatrice H. Tothill.

The Williams & Wilkins Co.

$6.00 6 x 9; viii + 351 *Baltimore*

The authors "have endeavored to provide (1) an untechnical introduction to the study of leaf-mining insects, intelligible to the general reader; (2) an account

of their natural history sufficiently detailed to be useful to the working ecologist; and (3) lists of the leaf-miners, of their food plants, and of technical papers concerning them adequate for the needs of the specialist. Thus we have undertaken to make more available to students, the rich but hitherto widely scattered results of many excellent investigations in this interesting ecological field."

The order is a large one; but the authors have succeeded remarkably well in their endeavor.

REPORT OF EUROPEAN CORN-BORER CONTROL CAMPAIGN BY THE UNITED STATES DEPARTMENT OF AGRICULTURE *for the Period March 14, 1927 to October 31, 1927, Inclusive.*

Government Printing Office
Washington

5 ¾ x 9; 24 (paper)

(Copies may be obtained free as long as the supply lasts from the Bureau of Entomology, United States Department of Agriculture)

This report gives an account of the large scale clean-up campaign against the European corn borer conducted during 1927. The cost of the campaign to the Federal government was $8,460,629.81; no figures are given of State or local expenditure. Annual surveys to determine the amount of infestation showed that at the close of 1926 there were approximately nine borers per hundred plants; at the close of 1927, after the clean-up there were approximately fourteen borers per hundred plants. "It therefore is obvious that the marked decrease in multiplication and the general improvement in corn-borer conditions recorded throughout the clean-up area at the close of the growing season of 1927 must be attributed principally, if not entirely, to the clean-up campaign."

It seems to us barely possible that this "decrease in multiplication" may have had other contributing causes.

THE FROG. *A Laboratory Guide.*
By Waldo Shumway. *The Macmillan Co.*
90 cents *New York*

4 ⅞ x 7 ⅜; viii + 67

The misfortune of the frog is that it is a "nice clean animal, easy to dissect and admirably fitted for physiological experiment." On some great dramatist—we would elect George Bernard Shaw—should be enjoined the duty of writing the epic tragedy of its immolation on the altar of science. This little manual furthers efficient and systematic dissection of the creature by the beginning student. The anatomical features to be noted as he progresses inward are given serially and directions for drawing are appended. There is a chapter on histology and one on embryology. It is not illustrated.

THE FISHES OF THE FAMILIES POMACENTRIDAE, LABRIDAE, AND CALLYODONTIDAE, COLLECTED BY THE UNITED STATES BUREAU OF FISHERIES STEAMER "ALBATROSS," CHIEFLY IN PHILIPPINE SEAS AND ADJACENT WATERS. *Contributions to the Biology of the Philippine Archipelago and Adjacent Regions. Smithsonian Institution, United States National Museum, Bulletin 100, Vol. 7.*

By Henry W. Fowler and Barton A. Bean.
Government Printing Office
$1.00 *Washington*

6 x 9 ¼; viii + 525 (paper)

This first part of a report on the immense collection of fishes made in 1907–1910 by members of the U. S. Bureau of Fisheries in the Albatross consists of studies on the fishes of the families Pomacentridae, Labridae, and Callyodontidae. Representatives of these families came chiefly from the waters of the Philippine Islands, although adjacent localities are included to some extent.

This work has been done with the utmost care. Extensive color descriptions made from the living material, or as soon after death as possible, add greatly to the value of the report. Forty-nine plates (uncolored) and a detailed index complete the volume.

THE SUGAR-CANE MOTH BORER IN THE UNITED STATES. *United States Department of Agriculture Technical Bulletin No. 41.*

By T. E. Holloway, W. E. Haley, U. C. Loftin and Carl Heinrich.

Government Printing Office

25 cents *Washington*

5 ¾ x 9 ¼; 77 + 2 plates (paper)

A description of the sugar cane moth borer (*Diatraea saccharalis*), with especial reference to its economic importance. It contains an account of the anatomy of the insect, as larva, pupa, and adult; the life cycle; natural means of control; and methods of artificial control. Indications are that the most effective method of control is the plowing under of the trash, rather than burning it, which is the procedure ordinarily used by the sugar planters. The authors' main objection to burning appears to be that it is more efficient as a means of destroying the egg parasites than the borers.

TRAITÉ DE ZOOLOGIE. *Fascicule VIII publié avec le concours de Rémy Perrier. Développement Embryogénique des Vertébrés Allantoidiens les Reptiles.*

By Edmond Perrier. *Masson et Cie*

40 francs *Paris*

6 ⅜ x 10; 2885–3115 (paper)

Since the death of Prof. Edmond Perrier in 1921 the editing of the remaining parts of his *Traité de Zoologie* has been taken over by his brother Rémy Perrier. The volume on batrachians appeared in 1925, and now we have the one on reptiles, which is preceded by a brief general account of the main features of the embryology of amniotic vertebrates. This is to be soon followed by volumes on the birds and mammals. When completed the whole will be a valuable addition to the basic text-book literature of zoology.

A STUDY OF PHYLLOXERA INFESTATION IN CALIFORNIA AS RELATED TO TYPES OF SOILS. *United States Department of Agriculture Technical Bulletin No. 20.*

By R. L. Nougaret and Macy H. Lapham.

Government Printing Office

10 cents *Washington*

5 ¾ x 9 ¼; 39 (paper)

The conclusion of this investigation into one aspect of the important question of the infestation of grape vines by *Phylloxera*, confirms previous general observation. Infestation rarely occurs upon soils of sandy texture and of loose porous structure, while it is most frequent where the soils are heavy, and become sticky when wet and bake and check when dry. The latter type probably affords more crevices and interstices for free movement of the insect. The study was executed on the vineyards of Fresno and Tulare Coun-

ties, California, which embody the most important types of soil in the State.

FUR-FARMING FOR PROFIT.
By Frank G. Ashbrook.

The Macmillan Co.
$4.00 *New York*
5 ¼ x 7 ¾; xxiii + 300

This book is written by one who has studied fur-farming from all angles. It contains much material of interest both to those engaged in this interesting field and to those contemplating entering it. The methods of raising the different animals, handling the pelts, marketing the furs, as well as reasons for success or failure are discussed. There is also a short chapter on legal considerations.

BIOLOGICAL AND TAXONOMIC INVESTIGATIONS ON THE MUTILLID WASPS. *Smithsonian Institution United States National Museum Bulletin 143.*
By Clarence E. Mickel.

Government Printing Office
65 cents *Washington*
6 ¼ x 9 ¾; ix + 351 (paper)

A detailed study of Mutillid wasps consisting of four parts: (1) Biology of the Mutillid wasps, (2) Type species of the genera of the family Mutillidae, (3) Monograph of the Mutillid wasps of the genus *Dasymutilla* occurring in America, north of Mexico, and (4) an annotated bibliography. Five plates and an index complete the volume.

WILD ANIMAL PETS.
By William L. Finley and Irene Finley.

Charles Scribner's Sons
$3.00 5 ¾ x 8; xiv + 311 *New York*

In this entertaining book is described the behavior of some twenty-four wild animals that were on a more or less social footing with the writers. The senior author, with many years of service as biologist and game warden of the State of Oregon, and his associate, have much to relate that will be of interest to people of all ages, but especially to the young who love the forests and the wild. There are numerous illustrations.

THE GIRAFFE IN HISTORY AND ART.
By Berthold Laufer.

Field Museum of Natural History
75 cents 5 ½ x 8 ½; 100 (paper) *Chicago*

In this little booklet the author gives many interesting facts concerning that oddly, not to say incredibly, constructed animal, the giraffe. The position which the giraffe has occupied in the art of the various peoples, from prehistoric times up to the present, is admirably shown by numerous illustrations. By no means the least interesting of these is a photograph of four superb creatures—prisoners in a kraal in their native country.

THE BOOK OF BIRDS. *Birds of Town and Country, the Warblers, and American Game Birds.* Contains the following: *Foreword*, by Gilbert Grosvenor; *Common Birds of Town and Country, Friends of Our Forests—the Warblers, and American Game Birds*, by Henry W. Henshaw; *How Birds Can Take Their Own Portraits*, by George Shiras, 3rd; *Encouraging Birds Around the Home*, by Frederick H. Kennard; *Our Greatest Travelers—Migratory Birds*, by Wells W. Cooke; *The World Record for Feathered*

Friends, and Bird Banding, the Telltale of Migratory Flight, by E. W. Nelson.

National Geographic Society
$3.00 *Washington*

6 ⅝ x 9 ⅝; 252

"In this revised volume are presented the principal articles and the most beautiful color illustrations of man's feathered friends which have been published in the National Geographic Magazine during the last thirteen years. The text and pictures comprise an authoritative and fascinating contribution to popular science."

STUDIES IN TROPICAL WASPS—THEIR HOSTS AND ASSOCIATES (*with Descriptions of New Species*). *Entomological Series Bulletin No. 19.*
By Francis X. Williams.

Experiment Station of the Hawaiian Sugar Planters' Assoc.
$2.00 *Honolulu*

6 ⅞ x 10 ¼; 179 (paper)

Interesting notes, fragmentary, but not superficial, of the author's observations on wasps and their associates in limited regions of Queensland, Australia, the Philippine Islands, Ecuador, British Guiana and Brazil. There are a considerable number of diagrammatic illustrations, some photographs, and an index.

BOLLES LEE'S MICROTOMIST'S VADE MECUM. *A Handbook of the Methods of Microscopic Anatomy. Ninth Edition.*
Edited by J. Brontë Gatenby and E. V. Cowdry, with the collaboration of W. R. G. Atkins, Sir William Bayliss, J. Thornton Carter, Robert Chambers, W. Cramer, C. Da Fano, Helen Pixell-Goodrich, J. G. Greenfield, Reginald Ludford, and G. Payling Wright, F. W. Rogers Brambell.

P. Blakiston's Son and Co.
$7.50 *Philadelphia*

5 ⅜ x 8 ¾; x + 710

The ninth edition of this standard handbook of microscopic anatomy has been thoroughly revised and somewhat enlarged. There are new sections by Dr. Robert Chambers and Dr. W. R. G. Atkins. All students of histological technique will, as always, find this book an indispensable asset.

AN INTRODUCTION TO THE TECHNIQUE OF SECTION-CUTTING. *From the Notes of the Late Mr. Peter Jamieson. Edited by Frances M. Ballantyne.*

E. and S. Livingstone
3 shillings net *Edinburgh*

4 ⅞ x 7 ¼; 80

This book presents a connected account of the essentials of section cutting and staining, freed from the accumulation of detail to be found in the standard texts. For the beginner, it provides the foundation of a sound technique, and should be a valuable introduction to the subject.

QUANTITATIVE STUDY OF THE CHANGES PRODUCED BY ACCLIMATIZATION IN THE TOLERANCE OF HIGH TEMPERATURES BY FISHES AND AMPHIBIANS. *From Bulletin of the Bureau of Fisheries, Vol. XLIII, 1927, Part II. Document No. 1030.*
By Edward S. Hathaway.

Government Printing Office
10 cents *Washington*

7 ½ x 11; 24 (paper)

A careful study of the temperature tolerance of animals representing five

different species. The results, which are given in detail, include a number of diagrams for each species studied exhibiting the effects of the varying temperatures on the different animals. A bibliography is appended.

FISHES OF CHESAPEAKE BAY. *Bulletin of the United States Bureau of Fisheries Vol. XLIII, 1927. Part I.*
By Samuel F. Hildebrand and William C. Schroeder. *Government Printing Office*
$1.50 7½ x 10½; 366 *Washington*

A general account of the fishes of Chesapeake Bay with a systematic catalogue by classes and subclasses. There is a glossary of terms and a bibliography, but an index is lacking.

THE AMERICAN BATS OF THE GENERA MYOTIS AND PIZONYX. *Smithsonian Institution, United States National Museum, Bulletin 144.*
By Gerrit S. Miller, Jr. and Glover M. Allen. *Government Printing Office*
55 cents *Washington, D. C.*
6 x 9¼; viii + 218 (paper)

An exhaustive taxonomic account, indexed by generic, specific, and subspecific names.

A SERIES OF EIGHT RADIO TALKS ON ZOOLOGY, OLD AND NEW. (*With Select Bibliography.*) *Radio Publication No. 39.*
By Robert T. Hance.
University of Pittsburgh
5⅞ x 9⅛; 85 (paper)

Does one see a foreshadow of the university's doom in this booklet of radio talks? It represents the 39th radio publication issued by the University of Pittsburgh. Glancing through it we learn that under such headings as Animals that Never Were; Animals that Might Have Been; Natural History of Long Ago; A Muddled World of Living Things; Animals the Ancients Never Dreamed of; Through the Microscope; Wanderers of the Sea; and On the Trail of the Unknown, with a *Select Bibliography* as a final flourish, zoology was presented to the world at large from the University of Pittsburgh Studio of KDKA.

BOTANY

DER WASSERHAUSHALT ÄGYPTISCHER WÜSTEN- UND SALZPFLANZEN. *Vom Standpunkt einer Experimentellen und Vergleichenden Pflanzengeographie aus.*
By Otto Stocker. *Gustav Fischer*
12 marks 6½ x 9⅝; 200 (paper) *Jena*

This volume on the water regulation of desert and salt marsh plants is a good example of the trend of modern biology towards physico-chemical exactness in its observation and experimentation. Ecology can no longer be regarded as a pleasant pastime, to be cultivated as a means of taking the boredom out of long railway journeys and the like. The elaborateness of the physical and chemical measurements of environment and plants in this thorough study is impressive.

Many of the results are of great biological interest, but space is lacking to review them all here. For example the author finds that in these desert and salt plants of Egypt, with which he is dealing, the structural type of the plant itself is of greater importance than has been gener-

ally recognized in managing the water regulation. He shows that the fluctuation in surface transpiration of the single plant type from habitat to habitat is far less than that within the single habitat from plant type to plant type.

Altogether this book must be regarded as a contribution of first rate importance to the literature of ecology. There is an extensive bibliography but no index.

ELEMENTARY BACTERIOLOGY. *By Joseph E. Greaves and Ethelyn O. Greaves.* *W. B. Saunders Co.*

$3.50 5¼ x 7¾; 506 *Philadelphia*

This book is designed for use as an elementary textbook. It will also be of use as a handbook of information to nurses, home demonstrators, agricultural and home economic workers, etc. The authors have succeeded in maintaining simplicity throughout, and have even excluded much of the ordinary garb of a textbook. There is very little that will be formidable to the lay reader. As comparatively little space is occupied with the illustrations, of which there are 129, the authors have succeeded in giving in the 500 pages a well rounded and entertaining picture of the science of bacteriology as it stands today. There is an index appended.

FACTORS OF SPREAD AND REPRESSION IN POTATO WART. *United States Department of Agriculture Technical Bulletin No. 56.*

By Freeman Weiss and Philip Brierley.

Government Printing Office

5 cents 5⅞ x 9; 14 (paper) *Washington*

The results of experimental investigations on the potato-wart fungus (*Synchytrium endobioticum*), accumulated by the authors while the disease itself was all the time becoming of diminished importance through effective control at the centers of infection. The experiments presented bear on the means of dissemination of the sporangia, their viability under natural and artificial conditions, and the susceptibility of the resting spores to heat and certain disinfectants.

THE BOOK OF WILD FLOWERS. *An Introduction to the Ways of Plant Life, Together with Biographies of 250 Representative Species and Chapters on our State Flowers and Familiar Grasses.* Contains the following: *Exploring the Mysteries of Plant Life*, by William J. Showalter; *Our State Flowers*, by Gilbert Grosvenor; *Familiar Grasses and their Flowers*, by E. J. Geske and W. J. Showalter; *Plant Biographies*, by William J. Showalter; *Color Plates from Life*, by Mary E. Eaton and E. J. Geske.

National Geographic Society
Washington D. C.

6⅞ x 9⅝; 243

"An introduction to the ways of plant life together with biographies of 250 representative species and chapters on Our State Flowers and Familiar Grasses." The volume is beautifully illustrated with color plates.

DIE NATÜRLICHE GRUPPE DER DAVALLIACEEN (SM.) KFS. *unter Berücksichtigung der Anatomie und Entwicklungsgeschichte ihres Sporophyten.*

By Enrique Pérez Arbeláez.

Gustav Fischer

6 Marks 6⅜ x 9½; 96 (paper) *Jena*

A thorough taxonomic revision of a group of the Polypodiaceae, with an

abundance of morphological detail. There is a bibliography of 67 titles.

AMERICAN FORESTS AND FOREST PRODUCTS. *United States Department of Agriculture Statistical Bulletin No. 21. Prepared by the Forest Service.*

Government Printing Office
45 cents *Washington*
5 7/8 x 9 1/2; 323 (paper)

Statistics of forests, lumber production, pulp wood and paper production.

MORPHOLOGY

TRAITÉ D'EMBRYOLOGIE COMPARÉE DES INVERTÉBRÉS.
By C. Dawydoff. *Masson et Cie*
120 francs *Paris*
6 1/2 x 10; xiv + 930 (paper)

There has long been a need for a new and up-to-date textbook of reasonable size on invertebrate embryology. This need is now well met by this treatise of Dawydoff's. The presentation of the essential facts is simple and direct, and well adapted to student use. For each group there is a well chosen bibliography of original sources, by way of which teacher and student can go more deeply in the matter if they want to. The volume is, in effect, a French translation and adaptation by the author of a Russian text which he published in 1915. The book is illustrated with 509 text figures, and is well indexed. An English translation of it would make a welcome addition to our zoological teaching literature. But in the absence of such a translation every teaching zoological laboratory will want it on the shelves as a reference work.

OUTLINES OF SCIENTIFIC ANATOMY *for Students of Biology and Medicine. Designed to Supplement the usual Textbook Teaching.*
By Wilhelm Lubosch. Translated from the German by H. H. Woollard.

John Bale, Sons and Danielsson, Ltd.
21 shillings 6 x 9 3/4; 392 *London*

At the time the German edition was reviewed in a previous number of THE QUARTERLY REVIEW OF BIOLOGY it was suggested that there should be an English translation made of this important work. This has now been done. Except for certain omissions and slight modifications, the translator follows very faithfully the original text. Its form is excellent.

For the benefit of those who are unacquainted with the German edition it should be said that this is not a textbook, but has as its purpose to supply collateral reading to students who are engaged in the necessary task of becoming acquainted with the large mass of facts which a study of anatomy entails. The science of anatomy is presented within its widest limits, from the morphological standpoint, and the interest and enthusiasm of the student cannot help but be aroused by the fascinating setting in which the subject is placed.

This book furnishes excellent material for a seminar course.

A HANDBOOK OF HISTOLOGY.
By A. McL. Watson.

William Wood and Co.
$3.75 4 3/4 x 7 1/2; xi + 207 *New York*

A triumph of epitome. The leaves of this book are small, the print large, the spacing and illustrations generous. Withal the subject of muscle is covered in 4 pages, blood in 6, nerve in 6, epithelium

in 5, etc., with several somewhat longer chapters devoted to the other tissues. We fail to discern what good educational purpose is served by the superficiality, and didactic categorization that results from such condensation.

PHYSIOLOGY AND PATHOLOGY

TRAITÉ DE PHYSIOLOGIE NORMALE ET PATHOLOGIQUE. *Tome III. Physiologie du Foie et de l'Appareil Urinaire.* *By M. Chiray, L. Cuénot, Ch. Dubois, I. Pavel, F. Rathery, G.-H. Roger.*

Masson et Cie

70 francs 6 ½ x 9 ½; 751 *Paris*

TRAITÉ DE PHYSIOLOGIE NORMALE ET PATHOLOGIQUE. *Tome IV. Les Sécrétions Internes.*

By J.-E. Abelous, R. Argaud, M. Garnier, J. J. Gournay, E. Hédon, L. Hédon, R. Huguenin, P.-M. Laignel-Lavastine, J. Parisot, G. Richard, G. Roussy, L. C. Soula, A. Tournade, R. A. Turpin.

Masson et Cie

65 francs 6½ x 9½; 585 *Paris*

This comprehensive treatise when completed will contain 11 volumes, divided as follows:

I. *Physiologie Générale*
II. *Digestion*
III. *Fonctions Hépatiques et Excrétion*
IV. *Les Sécrétions Internes*
V. *Respiration*
VI. *Circulation*
VII. *Les Humeurs: Sang et Lymphe, Réactions d'Immunité*
VIII. *Physiologie Musculaire. Chaleur Animale*
IX et X. *Physiologie Nerveuse*
XI. *Reproduction et Croissance*

Separate subjects are dealt with by individual authors, who are men of authority in their respective fields in the Latin countries.

Vol. III on the physiology of the liver and urinary apparatus comprises the following chapters: Physiology of the liver, by G.-H. Roger; Physiology of the gall bladder and of the bile ducts, by Chiray and I. Pavel; The "livers" of invertebrates, by L. Cuénot; Excretion, by L. Cuénot; Physiology of the kidneys, by R. Rathery; Excretion of the urine, and prostate, by Ch. Dubois.

Vol. IV on internal secretions contains the following chapters: General study of the internal secretions, by J.-E. Abelous; Pancreas, internal secretion, by E. Hédon and L. Hédon; The spleen, by J.-E. Abelous, R. Argaud and L.-C. Soula; The thymus, by J. Parisot and G. Richard; Thyroid gland, by Garnier and R. Huguenin; The parathyroids, by Garnier and R.-A. Turpin; The pineal gland, by Laignel-Lavastine; Hypophysis and infundibular region, by G. Roussy et J. J. Gournay; Superrenals by A. Tournade.

The printing and illustrations are rather poor. An index for the whole work is promised when it is complete, but there is none for the individual volume.

FILTERABLE VIRUSES.

By Harold L. Amoss, Jacques J. Bronfenbrenner, Alexis Carrel, Edmund V. Cowdry, Rudolf W. Glaser, Ernest W. Goodpasture, Louis O. Kunkel, Stuart Mudd, Peter K. Olitsky, Thomas M. Rivers. Edited by Thomas M. Rivers.

The Williams & Wilkins Co.

$7.50 5¾ x 9; ix + 428 *Baltimore*

An attempt is here made to review our present knowledge of the biologic phenomena that are usually discussed under the head of filterable viruses. As the editor points out in his introductory article, our

ignorance concerning the nature of these organisms is great, and no authoritative systematic account is yet possible. What is done here is to collect the opinions of a number of investigators on aspects of the subject with which they have had special experience. They are the following: Thomas M. Rivers—Some General Aspects of Filterable Viruses; Stuart Mudd—Filters and Filtration; Alexis Carrel—Tissue Culture in the Study of Viruses; Edmund V. Cowdry—Intracellular Pathology in Virus Diseases; Harold L. Amoss—Virus Diseases of Man as Exemplified by Poliomyelitis; Peter K. Olitsky—Virus Diseases of Mammals as Exemplified by Foot-and-Mouth Disease and Vesicular Stomatitis; Ernest W. Goodpasture—Virus Diseases of Fowls as Exemplified by Contagious Epithelioma (Fowl-Pox) of Chickens and Pigeons; Rudolf W. Glaser—Virus Diseases of Insects; Louis O. Kunkel—Virus Disease of Plants; Jacques J. Bronfenbrenner—Virus Diseases of Bacteria—Bacteriophagy.

If the work as a whole seems to be characterized by a measure of vagueness and inconsistency, it is to be said that this is true too of the subject itself. There is an extensive bibliography appended to each article and an index for the entire volume. It should be of service to biologists who are curious to learn of what is being done in the realm of the tiniest of living beings.

TRAITEMENT BIOLOGIQUE (BIOTHÉRAPIE) DES INFECTIONS *par les Huiles Essentielles, les Résines (Oléorésinothérapie), et par les Essences Déterpénées, les Lipides (Oléolipothérapie).*

By Albert Jentzer. *Masson et Cie*

80 francs 6¾ x 9¾; 424 (paper) *Paris*

This is a detailed account of an extremely thorough investigation of certain new therapeutic agents, which, on the evidence presented, appear to be of great value in all pyogenic infections (staphylococcus, streptococcus, B. coli, etc.). The author is *Privat-docent* in surgery at the University of Geneva. "Themsaline," the first and more important of the agents tested, is a rectified and fractioned mixture of certain essential oils, which has in its final composition 7 per cent phenols, 12 per cent aldehydes, and 63 per cent terpenes. A full account is given of its preparation. It is administered intravenously. Its results in cases of pyogenic infections, abscesses, phlegmons and the like, are little short of marvellous. The author gives extensive clinical and experimental reports on themsaline. Another agent, which under certain indications may be used with themsaline, is "lipodeterpenol," which functions as an antigen. Space is lacking for more detailed review of this book here, but we commend it to the attention of pharmacologists, surgeons and medical men, with the statement that it bears all the earmarks of a thorough and sound piece of research. There is a bibliography of 499 titles.

ÜBER DAS PROBLEM DER BÖSARTIGEN GESCHWÜLSTE. *Eine Experimentelle und Theoretische Untersuchung.*

By Lothar Heidenhain. *Julius Springer*

28 marks (paper) *Berlin*

32 marks (cloth)

10 x 13; vi + 153

This beautifully printed and illustrated quarto monograph describes the author's researches on the cause of cancer. It proceeds from the working hypothesis that it should be possible so to destroy human tumors by lysis that the agent in them which causes cancer would not be destroyed. Then the lytic products of such

technique are to be injected into animals, and there should then be found in the body of such animals changes in the epithelial or connective tissue cells of carcinomatous or sarcomatous character. Heidenhain has tested this idea on 2521 mice, working with human tumors of various sites and histological types. The result is taken to confirm the hypothesis. In fact it was found that in white mice injected with derivates of human carcinoma (either primary or metastatic) or sarcoma, there appeared carcinomata or sarcomata. The author concludes that the relation between these events was causal, and concludes that cancer is an infectious disease.

This is a piece of work with which all students of the cancer problem will have to reckon.

COMPARATIVE PHYSIOLOGY OF THE HEART.

By A. J. Clark. *The Macmillan Co.*
$3.25 5¼ x 8⅜; v + 157 *New York*

The author of this volume devotes himself very largely to the comparative physiology of the vertebrate heart. After the introductory chapters the following aspects of the subject are treated: The properties of vertebrate heart muscle; the transmission of the excitatory process; the nervous control of the heart; influence of temperature on heart functions; the influence of body weight on the size of the heart in warm-blooded animals; the relation between circulation volume and body weight in warm-blooded animals; heart functions in cold-blooded animals and embryos; the work of the heart in relation to body weight in warm-blooded animals; and the influence of chemical environment on the heart's activity.

This book will be of interest to all research workers in biology, following as it does, the paths of many divergent lines of work. Each chapter is terminated with a bibliography. Included in the text are 49 tables and 15 figures. At the end of the book are three appendices containing various records on mammalian and bird hearts.

HISTORY OF THE PHYSIOLOGICAL SOCIETY DURING ITS FIRST FIFTY YEARS 1876–1926.

By Sir Edward Sharpey-Schafer.
Cambridge University Press
15 shillings net *London*
6½ x 9¼; 198 (paper)

At the meeting of March 21, 1925, of the Physiological Society of England, it was resolved that "Sir E. Sharpey-Schafer be asked to write a report on the foundation of the Society." The present volume is the result. It is a useful contribution to the contemporary history of science. The Physiological Society started as a dining club, and in some sense has always remained that. It has never had a president, and there is no provision in its statutes for any elaborate formal organization. The underlying motive which led to its formation was, aside from sociability, to provide some means for presenting a unified front on the part of experimental physiology against an impending legislative attack upon the practice of vivisection. The volume consists essentially of an abstract of the minute books of the Society, with brief running comments, largely biographical, by the author. It is thoroughly indexed.

COYOTILLO (KARWINSKIA HUMBOLDTIANA) AS A POISONOUS PLANT. *United States Department of Agriculture Technical Bulletin No. 29.*
By C. Dwight Marsh, A. B. Clawson and

G. C. Roe. *Government Printing Office*
10 cents *Washington*

5¾ x 9⅛; 26 (paper)

The subject of this bulletin is a shrub found in Texas and Mexico, and known since 1789 to possess poisonous properties. The effect of ingestion on cattle, sheep, goats, guinea pigs, and chickens, as shown by the prolonged experiments of the authors, is to produce a motor paralysis affecting chiefly the posterior limbs. The leaves as well as the fruit are toxic, but to different degrees. Symptomotology, toxicology and moto-pathology are considered, but nothing very enlightening as regards the character or location of the primary lesion.

ETUDES SUR L'IMMUNITÉ DANS LES MALADIES INFECTIEUSES.

By A. Besredka. *Masson et Cie*
30 francs *Paris*

5⅝ x 8¼; 404 (paper)

In this volume are collected some fifteen of the distinguished author's studies on various aspects of the problem of immunity, made during the past thirty years at the Pasteur Institute in Paris. Dr. Besredka somewhat apologizes for their apparent diversity, but points out that there is really a unifying element in that they all bear upon the problem of vaccination, preventive or curative. All students of immunity will be glad to have this material handily collected in a single volume.

L'INFECTION BACILLAIRE ET LA TUBERCULOSE CHEZ L'HOMME ET CHEZ LES ANIMAUX. *Processus d'Infection et de Défense. Étude Biologique et Expérimentale. Vaccination Préventive.*

By A. Calmette. With the collaboration of A. Boquet and L. Nègre. *Masson et Cie*
125 francs *Paris*

6½ x 10; 883 (paper)

The third edition in French of the definitive work by Calmette. The first edition in English translation was noted in these columns in an earlier number (Vol. I, No. 1). This issue is enlarged by the author with the assistance of A. Boquet and L. Nègre of the Institut Pasteur de Paris. The additions include an account of the work of foreign investigators and two notable chapters on active immunization with BCG.

PRACTICAL BACTERIOLOGY, BLOOD WORK AND ANIMAL PARASITOLOGY *including Bacteriological Keys, Zoological Tables and Explanatory Clinical Notes. A Compendium for Internists.*

By E. R. Stitt. *P. Blakiston's Son and Co.*
$6.00 *Philadelphia*

5¼ x 7¾; xv + 837

The eighth edition of this very useful standard laboratory manual has been thoroughly revised and enlarged and brought entirely up to date.

BIOCHEMISTRY

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 258.* Containing the following articles: *Die äquimensurale Ultraviolett- und Fluorescenz-photographie*, by Gustav Kögel; *Die Methodik zur Prüflung der Lichtempfindlichkeit der Naturfarbstoffe*, by Gustav Kögel; *Methodik der diagnostischen und therapeutischen Anwendung der Elektrizität*, by August Laqueur.

Urban und Schwarzenberg
10 marks 7 x 10; 172 (paper) *Berlin*

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 261. Elektronen- und Ionenröhren.*
By Ferdinand Schieminzky.
Urban und Schwarzenberg
25 marks 7 x 10; 442 (paper) *Berlin*

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 262. Methoden der Bioelektrostatik.*
By Rudolf Keller and Joseph Gicklhorn.
Urban und Schwarzenberg
5 marks 7 x 10; 92 (paper) *Berlin*

These new parts of the Abderhalden *Handbook* of biological technique deal with various aspects of biophysics. They are all valuable contributions, but are calculated to throw the old-fashioned naturalist into a fit of depression at the realization, which they emphatically drive home, that at least a part of biology has got away from him, hopelessly and irrevocably.

CREATINE AND CREATININE.
By Andrew Hunter.
Longmans, Green and Co., Ltd.
$5.00 6⅛ x 9⅝; vii + 281 *New York*

Creatinin stands in a unique position among excreted products in its probable relation to endogenous metabolism. While its great interest together with the chemically closely related creatin has long been recognized, their biochemistry remains obscure in most essential details. This volume adequately reviews our present knowledge of their chemistry and physiology and provides an extended bibliography. The recent fundamental experiments of Fiske and Subbarow indicating that creatin exists in the muscles as a labile compound with phosphorus awaken renewed interest in the subject and make this work especially timely.

A TEXT-BOOK OF BIOLOGIC ASSAYS.
By Paul S. Pittenger.
P. Blakiston's Son and Co.
$3.00 net *Philadelphia*
5¼ x 7¾; xxiii + 373

In this reissue, the subject matter of the first edition (former title *Biochemic Drug Assay Methods*) has been practically rewritten, in order to include the numerous advances made in methodology; and several new chapters and 64 new illustrations added in order to bring the manual up to date. Its purpose is to serve as a text book of biologic assay technique for students of pharmacy and medicine, and for those engaged in laboratories devoted to the biologic standardization of drugs.

OILS, FATS AND FATTY FOODS. *Their Practical Examination. A Handbook for the Use of Analytical and Technical Chemists and Manufacturers.*
By E. Richards Bolton (with a chapter on Vitamins by J. C. Drummond).
P. Blakiston's Son and Co.
$8.00 *Philadelphia*
6⅛ x 9¼; xvi + 416

This is a handbook for the use of technical chemists who are called upon to analyze edible oils and fats. The methods given are those which the author has found satisfactory. He has, in general, given only one method for any one purpose. After chapters on preliminary examination, on general analytical methods, and on the interpretation of analytical

methods, there follow chapters on specific products, such as butter and margarine, animal fats, vegetable oils and fats, cocoa and chocolate, and milk. There is a final chapter, by Drummond, on the nutritive value of fats and oils, with particular reference to vitamins.

LABORATORY MANUAL OF PHYSIOLOGICAL CHEMISTRY.
By Meyer Bodansky and Marion S. Fay.
John Wiley and Sons, Inc.
$2.00 5¾ x 9; 234 *New York*

Pedagogical experiments for the student in the classical course of physiological chemistry. The importance of dynamical concepts that is emerging from the modern investigations into the physical chemistry of the organism is not reflected in the examples. Neither sodium nor potassium is listed in the index.

STUDIES ON OXIDATION-REDUCTION. I–X. *Hygienic Laboratory Bulletin No. 151.*
By the Staff of the Division of Chemistry, Hygienic Laboratory, United States Public Health Service.
Government Printing Office
50 cents *Washington*
5⅞ x 9⅛; vi + 363 (paper)

The first ten papers on oxidation and reduction of Clark and his associates at the Hygienic Laboratory are here reprinted. The first two develop the essential equations for the electrode potentials, and the rest deal with specific organic oxidation-reduction systems. The whole work is of fundamental import for the understanding of the mechanics of living processes.

SEX

TECHNIQUE OF CONTRACEPTION. *The Principles and Practice of Anti-Conceptional Methods.*
By James F. Cooper. *Day-Nichols*
$7.50 *New York*
6⅛ x 9⅛; xvi + 271

The preface makes the following statement:

> The contents of this book and its technical presentation indicate clearly that it is written exclusively for the medical profession. Moreover, the author has specifically arranged with the publisher so that copies of the book will be available only to physicians, thus giving emphasis to his belief that all practical aspects of contraception should be under the direction of members of the medical profession.

The book contains one of the first attempts at a statistical investigation of the efficiency of contraceptive methods which has ever been published. (Dr. Marie Stopes' report on the first five hundred cases at her clinic is valueless because of the failure to follow up cases.) He reports 95 per cent successful cases out of a total of 806 patients who had been using the methods prescribed for a period of six months to two years. There is, however, no evidence to show how many babies these women would have had during the observed period of exposure to risk if they had *not* used the specified methods of contraception. The chief cause of failure was said to be carelessness; and we are inclined to wonder whether any higher percentage of success than that alleged could reasonably be expected in ordinary clinical experience. But what Cooper, and nearly all birth control propagandists, mean when they speak of "success" is merely that the women under observation did not become pregnant during the time they were observed. This fact, however, obviously is no proof that failure of conception was *caused* by the contraceptive technique employed.

GREFFE OVARIENNE ET ACTION ENDOCRINE DE L'OVAIRE. *Étude Histologique, Biologique, Clinique et Chirurgicale.*
By Vittorio Pettinari. *Gaston Doin et Cie*
70 francs 6¼ x 9½; 487 (paper) *Paris*

Works on ovarian and testicular grafts suffer in these times from the suspicion of the ordinary reader that probably here is another piece of quackery. One is disposed to be a little more severely critical than of a work in some other fields of research. With the ultimate validity of the author's conclusions we do not propose to deal here. Some of them sound plausible enough; others are rather more disturbing to our *a priori* sense of the fitness of things. We do wish, however, to regret that the author has not seen fit to describe in more detail the experimental evidence on which his conclusions rest, and particularly that he has stated so little as to the number of experiments involved. We find him stating that he has operated on 332 animals (over 350, he says, at the time of going to press); and this may be a large number, but its significance depends on the ground covered. Now he also makes some statements as to the nature of his experiments, and to the variables considered; and at rough computation, to cover completely the ground indicated, a total of something on the order of a thousand experiments would have been required, allowing only one for each combination of variables. Accordingly, in the absence of any statement of the extent of the experience on which any particular conclusion rests, one is somewhat at a loss for an indication as to the validity of any of the work.

Our general attitude of hesitancy is not lessened by the author's work on rejuvenation. His general conclusions agree with those of Voronoff; but as far as one can learn, the experimental basis on which they rest is very thin indeed.

The book is largely and well illustrated with drawings and photographs of ovarian sections. There is a bibliography, restricted, however, to the literature on actual ovarian grafts.

SEX DEVELOPMENT IN APES. *Comparative Psychology Monographs Vol. 5, No. 1.*
By Harold C. Bingham.
The Johns Hopkins Press
$2.50 7 x 10¼; 165 *Baltimore*

It has been noted by that eminent anthropologist, George Jean Nathan, as one of the folk beliefs of America, that when one takes one's best girl to the Zoo, the monkeys invariably do something that is very embarrassing. The present monograph is intended to substantiate that belief. It gives an extended account of the beginnings of sex behavior in the two pairs of young chimpanzees of the Yale Institute of Psychology, together with some observations on adults at the Abreu colony. The monograph is of great interest to psychologists, and, we regret to say, to laymen.

SEXUALTYP UND KULTUR. *Elemente einer Darstellung der europäischen Kulturgeschichte auf der Grundlage der vergleichenden Psychologie der Geschlechter. Abhandlungen aus dem Gebiete der Sexualforschung. Band V, Heft 3.*
By Ernst Klimowsky.
A. Marcus und E. Weber's Verlag
6 marks 6⅞ x 10; 80 (paper) *Berlin*

The author's position is that nearly all human beings are not wholly single-sexed, male or female, in the makeup of their personality, and particularly with reference to the psychological panel of personality, to use Draper's convenient

terminology. Klimowsky discusses in an interesting, if somewhat pedantic manner, the influence upon cultural history of these phenomena of human intersexuality, composite sexuality, etc. The work is heavily documented, there being some 125 notes to the literature.

PSYCHOLOGY AND BEHAVIOR

THE UNCONSCIOUS. *A Symposium.*
Alfred A. Knopf, Inc.
$2.50 5 x 7⅜; 260 *New York*

This book is the result of a symposium, held in Chicago under the auspices of the Illinois Society for Mental Hygiene, which had for its aim the study of the synthetic tendency in the unconscious. We read in the preface by Mrs. W. F. Dummer that it is by a "chewing of the mental cud" that scientific principles are formulated and poets inspired, as well as many of the very ordinary affairs of life regulated. Therefore "May we learn consciously to utilize this integrative action of the unconscious? May we find the basis of constructive ideation with resultant progressive behavior? Is thought process discoverable?"

The opening chapter is on "The Beginnings of Unity and Order in Living Things" by the well-known biologist, C. M. Child; followed by a paper "On the Structure of the Unconscious" by Kurt Koffka; The Genesis of Social Reactions in the Young Child, by John E. Anderson; The Unconscious of the Behaviorist, by John B. Watson; The Unconscious Patterning of Behavior in Society, by Edward Sapir; The Configurations of Personality, by W. I. Thomas; The Prenatal and Early Postnatal Phenomena of Consciousness, by Marion E. Kenworthy; Values in Social Psychology, by F. L. Wells; and Higher Levels of Mental Integration, by William A. White.

The various chapters make interesting reading although the reader is left with the impression that much violent "chewing of the mental cud" is still necessary if the unconscious is ever to be brought out into the open and consciously used as a means to an end. And even then, shall we not have just as many mentally inefficient people in the world, or, possibly even more? Would not Dr. Watson's plan produce a far greater crop of neurasthenics than we are already burdened with?

MORTON PRINCE AND ABNORMAL PSYCHOLOGY.
By W. S. Taylor. *D. Appleton and Co.*
$1.75 5 x 7⅜; xi + 137 *New York*

This is a brief connected account and summary of the theories of the leading American psychopathologist. It should be read by anyone who has read Freud and swallowed him whole.

MALARIAL PSYCHOSES AND NEUROSES *with Chapters Medico-Legal, and on History, Race Degeneration, Alcohol, and Surgery in Relation to Malaria.*
By William K. Anderson.
Oxford University Press
$13.00 7¼ x 9¾; viii + 395 *New York*

This treatise surveys the aspects of malaria that relate to its nervous manifestation. Dealing largely with matters of detail, the author succeeds nevertheless in retaining throughout a sense of the broad social interest of his subject. The more general deteriorating effects of the disease on society are first discussed, and then its minute neuro-pathology. Then

the psychic manifestations are considered *seriatim*, under the several classical psychopathological categories, by means of brief case histories. Neuropathology is similarly considered. The illustrations are not numerous, but the colored plates depicting the cellular pathology are superbly reproduced, and the style measures up to the high standard we have learned to expect in the Oxford publications. There are some thirty-five pages of references, and an index of authors and subjects.

GORILLA. *Tracking and Capturing the Ape-Man of Africa.*
By Ben Burbridge. *The Century Co.*
$3.50 5⅛ x 7⅞; xi + 323 *New York*

The portion of this book which will be of the greatest interest is that dealing with the author's expedition into the Belgian Congo, from which he brought back the only live gorillas in captivity. In particular, the young female, "Congo," who has been studied in considerable detail by Professor Yerkes, was captured by Mr. Burbridge. His account of the wild life of the gorilla is interesting, if not extensive. Aside from the gorillas, the book does not differ greatly from the ordinary account of African hunting trips.

BIRDS AT THE NEST.
By Douglas Dewar.
John Lane: the Bodley Head Ltd.
7 s. 6 d. 5 x 7⅜; 271 *London*

Douglas Dewar's books about birds always contain a good deal of material of general biological interest. The present volume is no exception to this rule. It discusses a considerable amount of material derived from the literature and from personal observations in the field regarding bird behavior, particularly with reference to the reproductive cycle. The net result of the discussion is to explode a great many rather widely held notions as to the intelligence of wild birds. The book is pleasantly written, and well indexed.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

THE NEW GENETICS.
By Glenn C. LaMaster. *Glenn C. LaMaster*
$1.50 *R.F.D. 2, Box 48, Akron, O.*
6 x 9; 80 (paper)

Those Ishmaelites in the society of science who bear the noble title of "cranks" are to be numbered among our few really independent intellects. Neither authority, nor accumulated wisdom, nor the rules of logic, stem the free movement of their thought. The emotional thrills that reward their anarchic rebelliousness must remain lost to the laboratory slave who has been taught to yield his most fundamental opinion to the position of a decimal point. But if he can overcome an habitual squeamishness, and plunge himself heartily into some of their literary products, he is certain to be rewarded by entertainment, and may occasionally pick up a fruitful idea.

The interest of this author in genetics springs from his occupation with poultry breeding on a farm near Akron, Ohio. His doctrines, if we may judge from references, are the product of some good reading and a lively imagination. We open to an introductory thesis, the guiding idea of the principles later enunciated. "The spermatozoon is the seedling of a new brain and nervous system, and that the

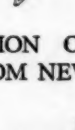
heart and venous system is given to the offspring by the mother parent." The writer considerately refrains from burdening the reader with too much evidence, but Fig. 2 goes far toward complete proof. It shows in sagittal section the human brain with its appended nerve cord tapering off as it winds caudally to a thin point; and in juxtaposition a pen sketch of a spermatozoon, the massive head merging into the long thin undulating body. "Its (the spermatozoon's) activity proves without question that it is endowed with consciousness." "Compare the shape and form of the brain and spinal cord with the shape and form of the spermatozoon." After a while in ontogeny "The spermatozoa bud off from the ends of the nerve branches in the glands after the same plan that seeds are produced upon the ends of the branches of trees." On the other hand, "The ova of the female bud off from a branch of the venous system in the ovaries." "Life begins with the union of the spermatozoon with the heart in rudimentary form. This union takes place in a microscopic sea where abound great numbers of basic body tissue cells which always exist in loose affinity in the germ plasm of both sexes." So we have acquired the nervous and vascular systems.

Now in respect to the several different kinds of cells that enter into the body organism other than the nervous and venous systems, how are they formed for the reproduction process? It seems very certain that these cells all exist in the germ plasm of both sexes. These cells which make up the main body structure are each one an independent life by itself. In the body structure they mass together in great bundles as we see in the muscles. But in the germ plasm of the glands these cells exist and multiply in loose affinity.

We go on to deeper matters, sex. "This difference of sex is determined by which unit, the venous system or the nervous system, first gains possession of the glands. Thus there is a struggle between these two units to determine which will dominate the sex of the embryo." After a clear explanation of Mendelism and segregation, we get the explanation of dominance.

Cells are of different kinds and from different individuals possess different degrees of vitality. And because of their different degrees of vitality and different traits of character, they have different rates of reproduction. And because of these differences some cells will divide twice as fast as others, and in some instances even greater differences in rate of reproduction may exist. . . . Suppose that two cells of different character start reproducing in the first stage of the embryo, and suppose that one cell possessing the factor which I will call the A factor reproduces twice as fast as the other cell which contains the B factor. . . . When we consider the fact that cell reproduction takes place at a very rapid rate and that there are many trillions of cells in an adult human body, it is plain that long before the body was mature the B factor would be completely obliterated from visible detection, and the A factor would appear as a dominant factor.

There is more of this, leading into practical advice to breeders of fowl and men, which we are unable to give for lack of space. Trained biologists will find some of these ideas novel, but this point is covered in the text. "The new facts of reproduction and inheritance are given to breeders here for the first time."



THE EVOLUTION OF SCIENTIFIC THOUGHT FROM NEWTON TO EINSTEIN.

By A. d'Abro. *Boni and Liveright*

$5.00 $5\frac{1}{2}$ x $8\frac{5}{8}$; xx + 544 *New York*

So far as may be judged by an amateur mathematician, this is the most satisfactory book issued for the layman to date on relativity and associated subjects. One must not conclude at once that it is altogether easy reading. To begin with it contains over 500 closely printed pages,

and the context is not always obvious at first glance.

> In the case of a fluid of the density of water, calculation shows that when the sphere of water had attained a radius of about 400 million kilometers, it would be impossible to increase its size further by adding more water to it. When this critical volume was reached, the fluid would fill the spherical space entirely. Moreover, calculation shows that the flow of time would be arrested altogether at the surface of the fluid, so here again we have another reason which would prevent the sphere from growing any larger.

But it is thorough; the author appears to have a real grasp of his mathematics, and he has an instinct for what will be the logical difficulties of the careful general reader. We are personally grateful for relief on one point that has oppressed us ever since we read an account by Einstein himself. It will be recalled that according to the Special Theory, in a system B moving with constant velocity relative to A, time is slowed up, so that an individual on B will appear younger than his twin brother on A. But these relationships are reversible and the individual on A will appear the younger from the viewpoint of B. It occurred to us therefore that if B took a trip around a circle and returned to A, when the brothers met they would be younger than each other. The dilemma is considered at length by the author, and the difficulty is resolved when it is realized that to travel in a circle B would have to accelerate, and acceleration takes us into the General Theory. Here it is not legitimate to make arbitrary transfers of the axes of reference. An accelerating system stands in a unique position and one may not transfer to such a system without positing a gravitational field. When this is done all calculaitons are consistent. B is younger from either viewpoint.

This should interest biologists. It appears to say that if an organism gets itself surrounded by a gravitational field, its life processes will all be slowed up. And since (so it appears to us) this must be due to physical forces, it becomes conceivable that one may influence the rate of life by physical means. The speculation serves as a corrective of another error, readily made by the reader of superficial accounts of relativity, namely that it is essentially only a matter of viewpoint that is involved. The fact is that if relativity be true, not only are our conceptions profoundly affected, but the physical world is fundamentally and actually different.

The inherent difficulty of the reading is aggravated by the poor and small print of the book, and the lack of an index is a serious defect.

THE RÔLE OF SCIENTIFIC SOCIETIES IN THE SEVENTEENTH CENTURY.

By Martha Ornstein.

The University of Chicago Press

$3.00 6 x 8⅞; 308 *Chicago*

This book is an interesting one and an important one. It was originally written as a Ph.D. thesis in 1913, and is now being republished. Its rescue from the usual fate of Ph.D. theses is fortunate.

The seventeenth century saw the organization of the earliest of the scientific societies. The present volume is an attempt to show how and why they came into existence, and to estimate their importance in the advancement of earning. Briefly, the author shows how science at the beginning of the century was in the hands of individual scientists, working for the most part in isolation; how, with the rapidly increasing interest in science, and particularly in experiment, little groups of men began meeting to discuss their investigations; and how these groups developed into corporate bodies, publishing

their results in their journals. There is a concluding chapter on the universities, showing how, except in Northern Italy and Holland, they were almost as little interested in science at the end of the century as they had been at the beginning.

Whether the author's judgments are in all cases sound is a matter on which opinions will differ. She has, for example, a higher opinion of Francis Bacon than, say, has Augustus de Morgan; and we suspect that she would rate the value to science of original research somewhat higher than would, say, Dr. William Morton Wheeler. Such points as these, however, do not affect the high value of the book.

There is a good bibliography and index.